

Upper Cretaceous ammonites from the Calabar region, south-east Nigeria

P. M. P. Zaborski

Department of Geology, University of Ilorin, P.M.B. 1515, Ilorin, Nigeria

Contents

Synopsis	2
Introduction	2
Systematic descriptions	5
Family Gaudryceratidae Spath	5
Genus <i>Anagaudryceras</i> Shimizu	5
<i>Anagaudryceras involvulum</i> (Stoliczka)	7
Genus <i>Gaudryceras</i> Grossouvre	8
<i>Gaudryceras beantalyense</i> Collignon	8
<i>Gaudryceras varicostatum</i> van Hoepen	10
Family Turrilitidae Meek	10
Subfamily Turrilitinae Gill	10
Genus <i>Turrilites</i> Lamarck	10
Subgenus <i>Turrilites</i> Lamarck	10
<i>Turrilites</i> (<i>Turrilites</i>) <i>scheuchzerianus</i> Bosc	10
<i>Turrilites</i> (<i>Turrilites</i>) <i>costatus</i> Lamarck	10
<i>Turrilites</i> (<i>Turrilites</i>) <i>acutus</i> Passy	11
Subfamily Nostoceratinae Hyatt	11
Genus <i>Pseudoxybeloceras</i> Wright & Matsumoto	11
Subgenus <i>Parasolenoceras</i> Collignon	11
<i>Pseudoxybeloceras</i> (<i>Parasolenoceras</i>) aff. <i>splendens</i> Collignon	13
Genus <i>Didymoceras</i> Hyatt	14
<i>Didymoceras</i> aff. <i>hornbyense</i> (Whiteaves)	14
<i>Didymoceras</i> aff. <i>cheyennense</i> (Meek & Hayden)	17
Family Desmoceratidae Zittel	17
Subfamily Puzosiinae Spath	17
Genus <i>Puzosia</i> Bayle	17
Subgenus <i>Anapuzosia</i> Matsumoto	17
<i>Puzosia</i> (<i>Anapuzosia</i>) cf. <i>dibleyi</i> (Spath)	17
Family Pachydiscidae Spath	19
Genus <i>Pachydiscus</i> Zittel	19
Subgenus <i>Pachydiscus</i> Zittel	19
<i>Pachydiscus</i> (<i>Pachydiscus</i>) <i>egertoni</i> (Forbes)	19
<i>Pachydiscus</i> (<i>Pachydiscus</i>) <i>dossantosi</i> (Maury)	20
Family Forbesiceratidae Wright	22
Genus <i>Forbesiceras</i> Kossmat	22
<i>Forbesiceras subobtectum</i> (Stoliczka)	22
<i>Forbesiceras obiectum</i> (Sharpe)	22
Family Acanthoceratidae Grossouvre	26
Subfamily Mantelliceratinae Hyatt	26
Genus <i>Sharpeiceras</i> Hyatt	26
<i>Sharpeiceras laticlavium</i> (Sharpe) <i>nigeriense</i> subsp. nov.	26
Genus <i>Acompsoceras</i> Hyatt	29
<i>Acompsoceras calabarensense</i> sp. nov.	29
<i>Acompsoceras</i> aff. <i>renevieri</i> (Sharpe)	30

Genus <i>Pseudocalycoceras</i> Thomel	30
<i>Pseudocalycoceras</i> cf. <i>haughi</i> (Pervinquière).....	30
Genus <i>Calycoceras</i> Hyatt	32
Subgenus <i>Newboldiceras</i> Thomel	32
<i>Calycoceras</i> (<i>Newboldiceras</i>) <i>annulatum</i> Collignon	32
Subfamily Acanthoceratinae Grossouvre	33
Genus <i>Acanthoceras</i> Neumayr	33
<i>Acanthoceras robustum</i> Crick	33
<i>Acanthoceras amphibolum</i> Morrow	35
<i>Acanthoceras</i> sp.....	38
Subfamily Euomphaloceratinae Cooper.....	39
Genus <i>Euomphaloceras</i> Spath	39
<i>Euomphaloceras inerme</i> (Pervinquière)	40
<i>Euomphaloceras cunningtoni</i> (Sharpe)	42
<i>Euomphaloceras cunningtoni meridionale</i> (Stoliczka)	43
<i>Euomphaloceras cunningtoni cunningtoni</i> (Sharpe)	45
<i>Euomphaloceras cunningtoni alatum</i> subsp. nov.	49
Genus <i>Kamerunoceras</i> Reymont	51
<i>Kamerunoceras tinrhertense</i> Collignon	51
Family Coilopoceratidae Hyatt	53
Genus <i>Coilopoceras</i> Hyatt	53
<i>Coilopoceras</i> aff. <i>newelli</i> Benavides-Cáceres.....	55
Family Sphenodiscidae Hyatt	57
Genus <i>Sphenodiscus</i> Meek	57
<i>Sphenodiscus lobatus</i> (Tuomey) <i>costatus</i> Zaborski	57
Correlation and palaeogeography	58
Acknowledgements	63
References	63
Note added in proof	69
Index	70

Synopsis

Ammonites of Cenomanian, Turonian, Campanian and Maastrichtian age are described from the Calabar region of south-eastern Nigeria. The Albian-Turonian Odukpani Formation yields Lower Cenomanian ammonites including *Sharpeiceras laticlavium nigeriense* subsp. nov. and *Acompsoceras calabarensis* sp. nov., but these faunas are, as yet, poorly known. Middle Cenomanian forms are of a dominantly north-west European character with species of *Anagaudryceras*, *Turrilites*, *Forbesiceras* and *Euomphaloceras* in common. The *Euomphaloceras cunningtoni* group is represented by the stratigraphically successive subspecies *E. cunningtoni meridionale* (Stoliczka), *E. cunningtoni cunningtoni* (Sharpe) and *E. cunningtoni alatum* subsp. nov. Also present is the typically North American late Middle Cenomanian species *Acanthoceras amphibolum* Morrow. The genus *Pseudocalycoceras* indicates the presence of Upper Cenomanian, but most of this substage, as well as the uppermost part of the Middle Cenomanian, is probably absent. The Turonian part of the Odukpani Formation yields *Kamerunoceras* and *Coilopoceras*. The overlying Nkporo Shale contains an Upper Campanian fauna at its base, with species of *Gaudryceras*, *Pseudoxybeloceras* (*Parasolenoceras*), *Didymoceras*, *Pachydiscus*, *Libycoceras* and *Sphenodiscus*, while its upper part, with *Gaudryceras*, *Pachydiscus* and *Sphenodiscus*, is of Lower Maastrichtian age.

The Cenomanian forms provide a palaeobiogeographical link between the north-west European and Angolan faunas, indicating that faunal interchange between the North and South Atlantic Ocean was possible.

Introduction

To the north of Calabar in south-eastern Nigeria, a basement block, the Oban Massif, is flanked on its southern side by a series of Cretaceous sediments. This region is of particular interest as it contains the most complete sequence of marine Cenomanian strata exposed in Nigeria and, except for Angola, in any part of west coastal Africa. Although the late

Cenomanian saw the onset of a transgression that was to culminate during the early Turonian, Cenomanian environments in Nigeria are thought to have been mainly regressive. Marine uppermost Cenomanian containing *Euomphaloceras septemseriatum* (Cragin) occurs in the middle Benue Valley of central Nigeria (Offodile 1976, Offodile & Reyment 1976) and faunas from the north-east of the country, with *Metengonoceras dumbli* (Cragin) and diverse vascoceratids (Barber 1957), are at least partly of Cenomanian age (see also Hancock & Kennedy 1981: 537). Otherwise, marine Cenomanian is known only from the Calabar region where the Odukpani Formation (Reyment 1955, 1956, 1965) includes Middle and Lower Cenomanian. Separated from the Precambrian basement by a thick sequence of continental clastics (the Awi Formation, see Adeleye & Fayose 1978), the Odukpani Formation extends from the Albian at its base to the Turonian in its upper part. It consists of shales, calcareous shales and sandstones with occasional beds of limestone. A thick limestone close to the base of the formation is well exposed in a quarry at Mfamosing, north-east of Calabar (Fig. 2, inset); Förster (1978) and Förster & Scholz (1979) reported a diverse Upper Albian–Lower Cenomanian ammonite fauna from here. Reyment (1955, 1957) and Fayose (1977) have described ammonites from higher in the Odukpani Formation. In the Calabar region the Odukpani Formation is overlain unconformably by the Upper Campanian–Lower Maastrichtian Nkporo Shale which, although probably only partly of marine origin, also contains ammonites at certain levels. The succeeding sediments belong to the continental late Tertiary Benin Formation.

The Odukpani Formation and Nkporo Shale are well exposed in road cuttings north-west of Calabar (Figs 1, 2), where the material described here was collected. Both formations have a gentle regional dip to the south-west. The lower part of the Odukpani Formation is, however, affected by broad folds trending NE–SW, and faulting may also be present. Dips rarely exceed 10°. The exposed parts of the Odukpani Formation consist here mainly of grey shales, pyritic at the base but calcareous and including numerous thin limestones higher up. A well-developed limestone–shale sequence occurs close to the top of the formation and at its base are the remnants after dissolution of another prominent limestone horizon. The folding makes it difficult to estimate the thickness of the formation: Reyment (1965: 34) gave a thickness of about 1000 m (including the basal clastics of the Awi Formation) but this is perhaps an underestimate. The outcropping part of the Nkporo Shale is about 700 m thick, an account of this part of the section and its *Libycoceras* and *Sphenodiscus* fauna having been given by Zaborski (1982).

A full list of the ammonites collected in the present study (not necessarily in stratigraphical order) is given below. Apart from faunas 1 and 2, all are from cuttings on the Calabar–Ikot Ekpene road (Figs 1–2) and are localized according to their distances from Calabar using the mileposts as reference points. From the Odukpani Formation the following forms were obtained:

Fauna 1. Road cutting on the Calabar–Akamkpa road, 1.5 km north of the junction with the Calabar–Ikot Ekpene road: *Desmoceras* sp., *Sharpeiceras laticlavium nigeriense* subsp. nov., *Acompsocheras calabarensis* sp. nov.

Fauna 2. Road cutting on the Calabar–Akamkpa road, 1 km north of the junction with the Calabar–Ikot Ekpene road: *Puzosia* sp., *Acompsocheras* aff. *renevieri* (Sharpe), *A.* aff. *essendiensis* (Schlüter).

Fauna 3. 25.8 km from Calabar: *Forbesiceras* sp., indeterminate acanthoceratids.

Fauna 4. 27.9 km from Calabar: *Turrilites* (*T.*) *scheuchzerianus* Bosc, *T.* (*T.*) *costatus* Lamarck, *Forbesiceras subobtectum* (Stoliczka), *Euomphaloceras inerme* (Pervinquière), *E. cunningtoni meridionale* (Stoliczka).

Fauna 5. 28.3 km from Calabar: *Turrilites* (*T.*) *costatus* Lamarck, *Desmoceras* (*Pseudouhligella*) sp., *Euomphaloceras cunningtoni cunningtoni* (Sharpe).

Fauna 6. 29.3 km from Calabar: *Desmoceras* (*Pseudouhligella*) sp., *Forbesiceras obtectum* (Sharpe).

Fauna 7. 30.1 km from Calabar: *Desmoceras* (*Pseudouhligella*) sp., *Puzosia* (*Anapuzosia*) cf.

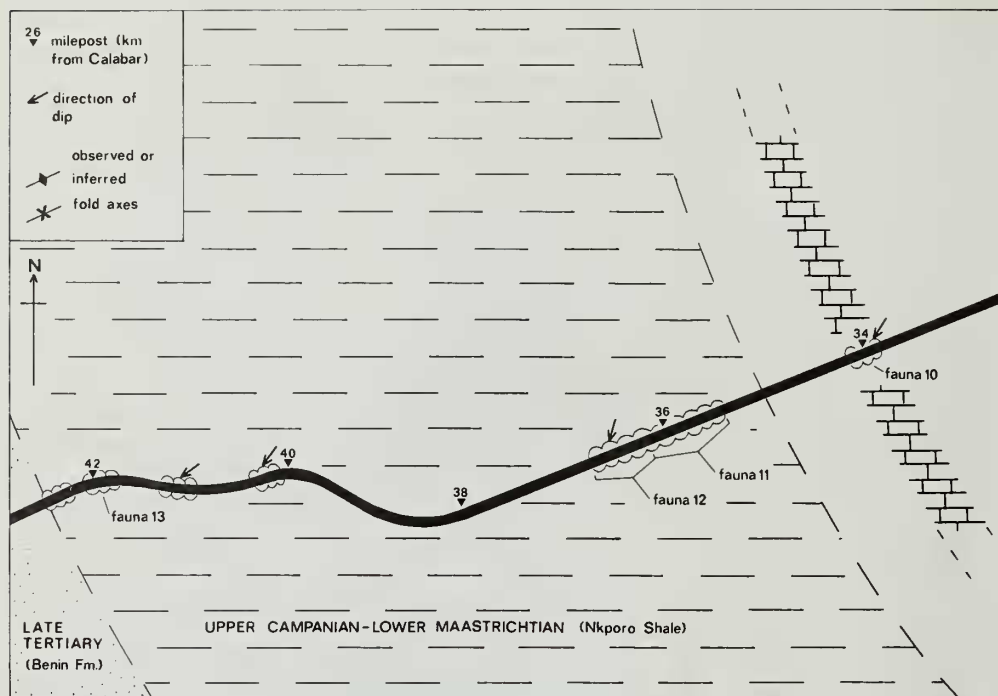


Fig. 1 Map showing road section north of Calabar and localities of fossils mentioned in the text: western portion.

dibleyi (Spath), *Forbesiceras obiectum*?, *Acanthoceras amphibolum* Morrow, *Acanthoceras* sp.

Fauna 8. 30.3 km from Calabar: *Anagaudryceras involvulum* (Stoliczka), *Turrilites* (T.) *acutus* Passy, *Forbesiceras obiectum*, *Calycoceras* (*Newboldiceras*) *annulatum* Collignon, *Euomphaloceras cunningtoni alatum* subsp. nov.

Fauna 9. 32.2 km from Calabar: *Acanthoceras robustum* Crick, *Euomphaloceras cunningtoni alatum*?

Fauna 10. 34 km from Calabar: *Puzosia* sp., *Kamerunoceras tinrhertense* Collignon, *Coilopoceras* aff. *newelli* Benavides-Cáceres.

In addition, there is a single specimen of *Pseudocalycoceras* cf. *haughi* (Pervinquière), of which the exact horizon within the Odukpani Formation is unknown.

From the Nkporo Shale the full list is:

Fauna 11. 35.5–36.3 km from Calabar: *Gaudryceras varicostatum* van Hoepen, *Pseudoxybeloceras* (*Parasolenoceras*) aff. *splendens* Collignon, *Didymoceras* aff. *hornbyense* (Whiteaves), *D.* aff. *cheyennense* (Meek & Hayden), *Baculites* sp., *Pachydiscus* (P.) *egertoni* (Forbes), *Libycoceras afikpoense* Reymont, *Sphenodiscus lobatus lobatus* (Tuomey).

Fauna 12. 36.3–36.7 km from Calabar: *Nostoceras* sp., *Libycoceras crossense* Zaborski.

Fauna 13. 42 km from Calabar: *Gaudryceras beantalyense* Collignon, *Baculites* sp., *Pachydiscus* (P.) *dossantosi* (Maury), *Sphenodiscus lobatus costatus* Zaborski.

These faunas add considerably to knowledge of Nigerian ammonite sequences and allow a more detailed correlation to be made with other parts of the world than has hitherto been possible. They also provide some palaeogeographical information on the opening of the South Atlantic Ocean and the extent of the late Cretaceous transgression in western Africa and the Sahara.

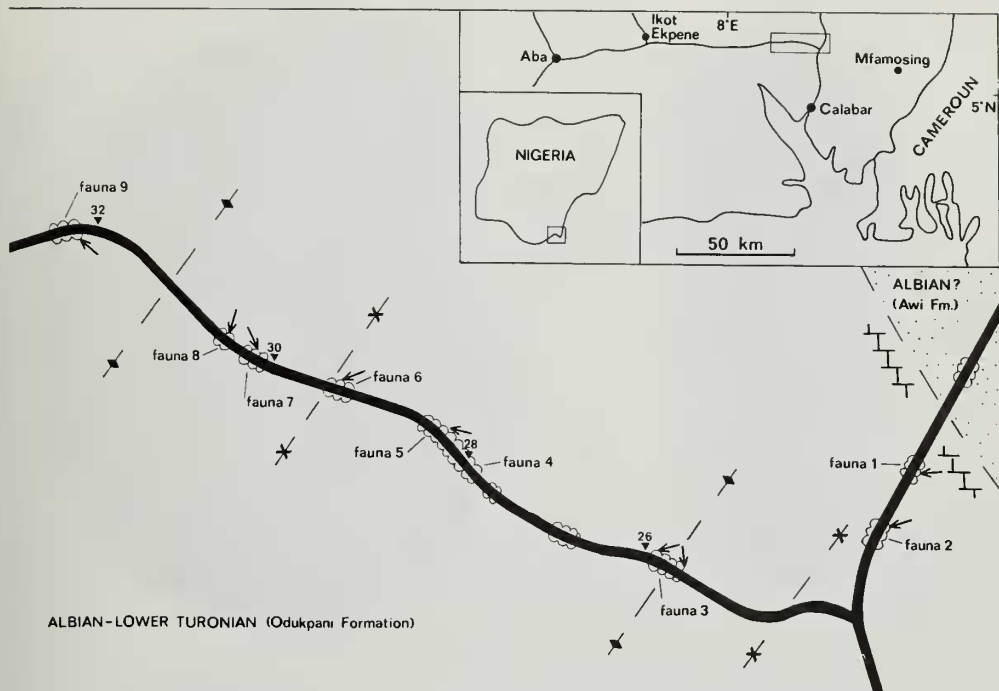


Fig. 2 Map showing road section north of Calabar and localities of fossils mentioned in the text: eastern portion.

Systematic descriptions

REPOSITORIES. Register numbers prefixed by the abbreviation UIN are of specimens in the Department of Geology, University of Ilorin, Nigeria. Those prefixed by the letter C. are of specimens in the Department of Palaeontology, British Museum (Natural History), London.

TERMINOLOGY. The following abbreviations are used. Dimensions (in mm): D, diameter; Wb, whorl breadth; Wh, whorl height; U, umbilical diameter. Whorl breadth and height are given for intercostal sections only. Figures in parentheses are dimensions as a percentage of the total diameter. Sutures: the terminology of Wedekind (1916), as revised by Wiedmann & Kullman (1981), is used. E, external lobe; L, lateral lobe; U, umbilical lobe; I, internal lobe. The terms 'inner' and 'outer ventrolateral tubercles' are used respectively for the *Treatise* (Arkell *et al.* 1957) terms 'lower' and 'upper ventrolateral tubercles'.

LOCALITIES. Unless otherwise stated, the material described is from cuttings on the Calabar-Ikot Ekpene road, south-east Nigeria. Certain specimens cannot be assigned with certainty to an exact horizon. Those that can are localized according to their distances from Calabar using the mileposts as reference points.

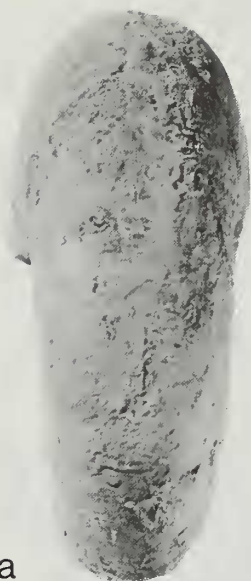
Superfamily **TETRAGONITACEA** Hyatt, 1900

Family **GAUDRYCERATIDAE** Spath, 1927

Genus **ANAGAUDRYCERAS** Shimizu, 1934

TYPE SPECIES. *Ammonites sacya* Forbes, 1846; by the original designation of Shimizu, 1934 (= *Ammonites buddha* Forbes, 1846, subj. syn.).

3a



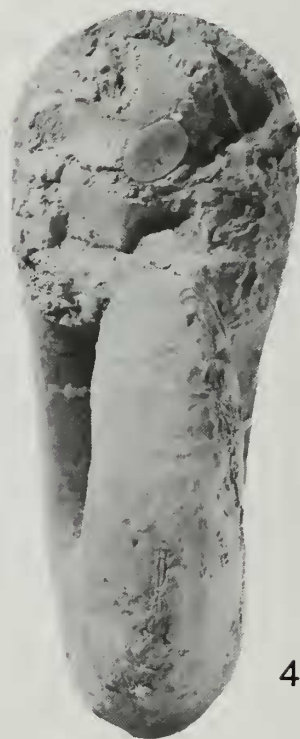
3b



4a



4b



Figs 3, 4 *Anagaudryceras involvulum* (Stoliczka). Odukpani Formation (Middle Cenomanian), 30.3 km from Calabar. Figs 3a, b, C.83113, $\times 1$. Figs 4a, b, C.83478, $\times 1$.

Anagaudryceras involvulum (Stoliczka, 1865)

Figs 3–4

- 1865 *Ammonites involvulus* Stoliczka: 150; pl. 75, figs 1a, 1b.
 1865 *Ammonites sacya* Forbes; Stoliczka: 154; pl. 76, fig. 3 (only).
 1895 *Lytoceras (Gaudryceras) involvulus* (Stoliczka) Kossmat: 32.
 1935 *Gaudryceras (Anagaudryceras) utaturense* Shimizu: 176.
 1956 *Anagaudryceras involvulum* (Stoliczka) Collignon: 68.
 1966 *Anagaudryceras involvulum* (Stoliczka); Howarth: 219; pl. 1, figs 1, 2.
 1975 *Anagaudryceras involvulum* (Stoliczka); Kennedy & Juignet: 77, fig. 1.
 1976 *Anagaudryceras involvulum* (Stoliczka); Juignet & Kennedy: 49; pl. 1, figs 1a–c, 2a–c.

MATERIAL AND OCCURRENCE. Three specimens (C.83113, C.83478, UIN 484.1) from the Odukpani Formation (Middle Cenomanian), 30.3 km from Calabar.

DIMENSIONS.	D	Wb	Wh	U
C.83113	90	36 (40)	39 (43.3)	26 (29)
C.83478	100	39 (39)	45 (45)	30 (30)
UIN 484.1	81	–	35 (43.2)	23 (28.4)

DESCRIPTION. These three fully septate specimens are evolute and moderately compressed, with the whorl sides rather flattened dorsally but converging ventrally to the broadly rounded venter. The whorls are a little higher than broad, at least at the largest preserved diameters. The umbilicus is moderately depressed, being a little less than one-third of the diameter in width. The umbilical shoulders are sharply rounded.

The shell in C.83113 is covered with very fine, dense, biconcave lirae which are coarsened at closely-spaced though irregular intervals. Where the shell is missing there are shallow, narrow constrictions taking the same path as the lirae. There are six constrictions on the last-preserved whorl but some are pronounced only on the ventral part of the whorl sides. They may be associated with very low, faint rib-like structures on the shell. In C.83478 and UIN 484.1 periodic deep constrictions associated with strong ribs appear at diameters in excess of 70–90 mm, and between these there are finer, more closely spaced ribs confined to the ventral half to two-thirds of the whorl sides.

The suture contains three saddles outside the umbilical shoulder. These are basically bifid with the two arms bifid again. In C.83113 L is deep and asymmetrically trifid but in C.83478 and UIN 484.1 it is shallower and less obviously trifid. There is a further small saddle between the umbilical shoulder and the umbilical seam but the internal suture is not displayed.

REMARKS. In recent discussions of *Anagaudryceras*, Howarth (1965: 357–358) and Kennedy & Klinger (1979: 144–146) divided the genus into two groups. The group of *A. buddha* (Forbes 1846: 112; pl. 14, fig. 9), a probable synonym of *A. sacya* (Forbes 1846: 113; pl. 14, fig. 10), includes forms developing strong fold-like ribs in the adult stages. The group of *A. involvulum* (Stoliczka 1865: 150; pl. 75, fig. 1; pl. 76, fig. 3) includes weakly ornamented species which may still develop periodic ribbing in the later stages; the present material falls into the second group. It is closest to the main Cenomanian species *A. involvulum*, which, although slightly more evolute, has a similar gross morphology and ornamentation, developing deeper constrictions and periodic ribbing towards adulthood (see Stoliczka 1865: pl. 76, fig. 3). As Howarth (1965: 358) has pointed out, a major problem in the subdivision of this genus is the lack of reliable information concerning intraspecific variation. Apart from the present material only a handful of specimens from the Cenomanian of southern India (Stoliczka 1865), the Middle Cenomanian of north-west France (Kennedy & Juignet 1975, Juignet & Kennedy 1976) and the mid-Turonian of Angola (Howarth 1966) have been referred to *A. involvulum*. The main variation between these specimens is in ornamental strength: some are weakly ribbed (Stoliczka 1865: pl. 76, fig. 3; Kennedy & Juignet 1975; Juignet & Kennedy 1976: pl. 1, figs 1a–c, 2a–c; C.83113, Fig. 3a, b herein); others develop

rather prominent ribbing in the later stages (Howarth 1966: pl. 1, figs 1, 2; UIN 484.1, C.83478, Fig. 4a, b herein).

A number of specific names are in use for post-Cenomanian members of the long-lived and conservative *A. involvulum* group (see list in Kennedy & Klinger, 1979: 146). Of these the Santonian *A. yamashitai* (Yabe 1903: 38; Matsumoto 1959: 138; pl. 37, figs 1a–d) is very like the Nigerian material. The Campanian–Maastrichtian *A. mikobokense* Collignon (1956: 59; pl. 8, fig. 1; Matsumoto 1959: 139; pl. 38, fig. 1; Howarth 1965: 358; pl. 4, figs 1–3) and *A. politissimum* (Kossmat 1895: 128; pl. 15, fig. 7; Collignon 1956: pl. 8, fig. 2) are also close but are distinctly more evolute, the latter being in addition more highly compressed.

Genus *GAUDRYCERAS* Grossouvre, 1894

TYPE SPECIES. *Ammonites mitis* Hauer, 1866; by the subsequent designation of Boule, Lemoine & Thévenin, 1906.

Gaudryceras beantalyense Collignon, 1956

Figs 5–6

1956 *Gaudryceras beantalyense* Collignon: 53; pl. 5, figs 1–3.

1965a *Gaudryceras beantalyense* Collignon; Collignon: 2; pl. 414, figs 1713, 1714.

MATERIAL AND OCCURRENCE. Nine specimens (C.82155–6, C.83203–4, C.83209, C.83508–10, UIN 439.1) from the upper Nkporo Shale (Lower Maastrichtian), 42 km from Calabar.

DIMENSIONS.	D	Wb	Wh	U
C.83203	115	42.5 (37)	53 (46)	35 (30.5)
C.83510	70	26 (37)	30 (43)	29 (41.4)

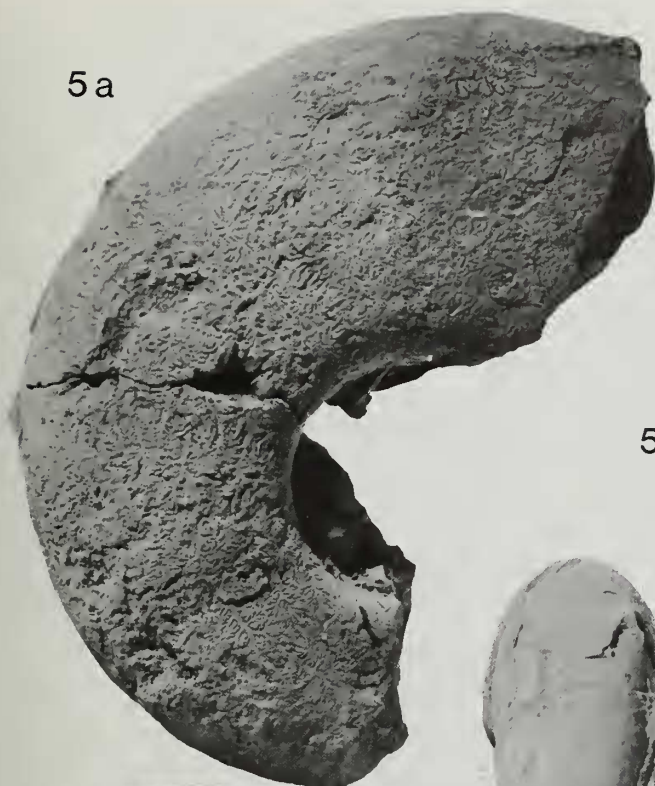
DESCRIPTION. In the earliest stages the whorls are depressed, being markedly broader than high. At a diameter of about 35 mm whorl breadth and whorl height are approximately equal. Thereafter the whorls become moderately compressed, higher than broad, with rather flattened flanks and a broadly rounded venter. The phragmocone reaches a diameter in excess of 150 mm. In the early stages the shell is highly evolute but at a diameter of about 40–45 mm the whorls become embracing and the shell increasingly involute. It is covered with dense, very fine ribs which are almost invisible to the naked eye. There are rather deep constrictions on internal moulds in the early stages, four being present on the last preserved half whorl in C.83510. In the later stages the constrictions become fainter and more widely spaced. At no stage do they seem to be associated with strengthened ribs, ornamental style remaining constant during ontogeny. Towards adulthood a septal lobe may develop.

REMARKS. Although a multitude of specific names have been proposed, three important groups can be distinguished within the genus *Gaudryceras* (see Howarth 1965: 360–362; Henderson 1970: 15–16; Kennedy & Klinger 1979: 128–129). The groups of *G. densiplicatum* (Jimbo 1894: 182; pl. 23, figs 1a, 1b) and *G. tenuiliratum* (Yabe 1903: 19; pl. 3, figs 3, 4) both include forms developing coarsely ribbed outer whorls. The third group, typified by *G. mite* (Hauer 1866: 305; pl. 2, figs 3, 4) and *G. varagureuse* (Kossmat 1895: 122; pl. 17, fig. 5; pl. 18, figs 2a–c), includes forms retaining fine ribbing throughout ontogeny. The present specimens belong in the last group but are peculiar in the extreme fineness of their ribbing and the lack of periodic strengthened ribs. In these respects, and also in gross morphology, they cannot be distinguished from the Malagasy species *G. beantalyense* Collignon (1956: 53; pl. 5, figs 1–3; 1965a: 2; pl. 414, figs 1713, 1714), although this is of Coniacian age. *G.*

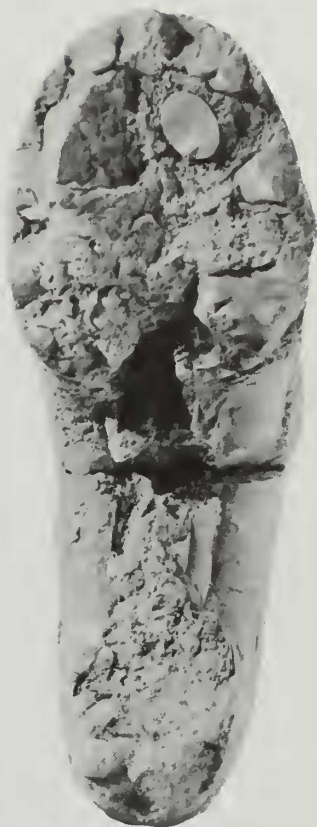
Figs 5, 6 *Gaudryceras beantalyense* Collignon. Upper Nkporo Shale (Lower Maastrichtian), 42 km from Calabar. Figs 5a, b, C.83203, $\times 1$. Figs 6a, b, C.83510, $\times 1$.

Fig. 7 *Turrilites (Turrilites) scheuchzerianus* Bosc. Odukpani Formation (Middle Cenomanian), 27.9 km from Calabar. C.82116, $\times 1$; note interruptions in ribs on lower half of whorl sides. See also Fig. 8.

5a



5b



7



6a



6b



analabense Collignon (1956: 54; pl. 6, figs 1–3; 1965a: 4; pl. 415, figs 1717, 1718), a contemporaneous form, is very close to *G. beantalyense* and may be a synonym.

Internal moulds of the outer whorls of the present material were previously misidentified (Zaborski 1982: 306, 323) as *Neodesmoceras* sp., which they closely resemble (compare, for example, Matsumoto & Saito 1954: 88; pl. 9, figs 1a–c; pl. 10, figs 1a–c; pl. 11, figs 1, 2). The discovery of the inner whorls, however, confirms the present identification.

***Gaudryceras varicostatum* van Hoepen, 1921**

1921 *Gaudryceras varicostatum* van Hoepen: 7; pl. 2, figs 10–12; text-figs 3, 4.

1922 *Gaudryceras cinctum* (Crick ms) Spath: 118; pl. 9, figs 3a, 3b.

1979 *Gaudryceras varicostatum* van Hoepen; Kennedy & Klinger: 133; pl. 3, figs 1–3; pl. 4; pl. 7, fig. 2; pl. 14, fig. 11; text-fig. 1 (with synonymy).

MATERIAL AND OCCURRENCE. Three specimens (C.83141–3) from the basal Nkporo Shale (Upper Campanian), about 36 km from Calabar.

REMARKS. These three fragmentary specimens, members of the *Gaudryceras mite* group, are all crushed and not worth figuring. On the later massive whorls their ornament consists of relatively strong, equally developed, sharp, biconcave lirae identical to that in *G. varicostatum* van Hoepen (1921: 7; pl. 2, figs 10–12; text-figs 3, 4), a species discussed in detail by Kennedy & Klinger (1979: 133). *G. varicostatum* is known from the Coniacian–Campanian of South Africa and the Malagasy Republic. The Campanian–Maastrichtian *G. propemite* Marshall from New Zealand (see Henderson 1970: 15; pl. 2, fig. 1) may be a synonym.

Superfamily TURRILITACEAE Meek, 1876

Family TURRILITIDAE Meek, 1876

Subfamily TURRILITINAE Gill, 1871

Genus TURRILITES Lamarck, 1801

Subgenus TURRILITES Lamarck, 1801

TYPE SPECIES. *Turrilites costata* Lamarck, 1801; by original designation.

***Turrilites (Turrilites) scheuchzerianus* Bosc, 1802**

Figs 7, 8

1802 *Turrilites Scheuzeriana* Bosc: 190.

1925 *Turrilites scheuchzerianus* Bosc; Diener: 84 (with synonymy).

1955 *Turrilites (Euturrilites) scheuchzerianus* Bosc; Reymont: 13; pl. 1, fig. 2.

1966 *Euturrilites scheuchzerianus* Bosc emend. Sharpe; Collignon: 24; pl. 12, fig. 1 (with synonymy).

MATERIAL AND OCCURRENCE. Fifteen specimens (C.82115–8, C.82124, C.82150, C.83093, C.85254, UIN 471.1–7) from the Odukpani Formation (Middle Cenomanian). UIN 471.1–471.7, C.83093 and C.85254 are from a horizon exposed 27.9 km from Calabar; the remainder, although not precisely localized, are almost certainly from the same level.

REMARKS. This well-known species is represented by variable material. The ribs often tend to be interrupted in the early whorls but are usually entire and slightly curved in the later stages. There are, however, a few individuals which at adulthood show one or two interruptions in the ribs on the lower half of the whorls, these specimens thus being intermediate between *T. scheuchzerianus* and *T. costatus* Lamarck: see below.

***Turrilites (Turrilites) costatus* Lamarck, 1801**

Figs 9, 10

1801 *Turrilites costata* Lamarck: 102.

1925 *Turrilites costatus* Lamarck; Diener: 81 (with synonymy).

1957 *Turrilites (Turrilites) costatus* Lamarck; Reymont: 56; pl. 9, fig. 3.

- 1962 *Turrilites costatus* Lamarck; Wiedmann: 192 (with synonymy).
 1971 *Turrilites (Turrilites) costatus* Lamarck; Kennedy: 30; pl. 6, fig. 3; pl. 8, figs 12, 14.
 1976 *Turrilites (Turrilites) costatus* Lamarck; Juignet & Kennedy: 63; pl. 3, figs 16, 18, 19 (with synonymy).

MATERIAL AND OCCURRENCE. Twenty-four specimens (C.83103–4, C.83467–71, C.85252–3, UIN 421.1–15) from the Odukpani Formation (Middle Cenomanian). C.85252 and C.85253 are from a horizon exposed at 27.9 km from Calabar, the remainder at 28.3 km from Calabar.

REMARKS. This species occurs at two horizons. The specimens (C.85252, C.85253) found at 27.9 km from Calabar accompany the material referred above to *Turrilites scheuchzerianus*, which, as mentioned, includes *T. costatus*-like variants. In these two individuals, rib subdivision is pronounced and they must be referred to *T. costatus*. The second and larger population occurs slightly higher, at 28.3 km from Calabar. Its members are morphologically highly variable, rib development on the upper whorl sides being markedly inconsistent. The population is, in fact, almost exactly intermediate in mean structure between *T. costatus* and *T. acutus* Passy. Some variants show the long ribs typical of the former species, others are like *T. acutus* in showing more rudimentary ribs.

***Turrilites (Turrilites) acutus* Passy, 1832**

- 1832 *Turrilites acutus* Passy: 334; Atlas p. 7; pl. 16, figs 3, 4.
 1925 *Turrilites acutus* Passy; Diener: 79 (with synonymy).
 1965 *Turrilites (Turrilites) acutus* Passy; Clark: 54; pl. 19, fig. 7 (with synonymy).
 1971 *Turrilites (Turrilites) acutus* Passy; Kennedy: 30; pl. 7, figs 7, 8.
 1976 *Turrilites (Turrilites) acutus* Passy; Juignet & Kennedy: 65; pl. 3, fig. 6; pl. 4, figs 1–3 (with synonymy).

MATERIAL AND OCCURRENCE. A single specimen (C.83114) from the Odukpani Formation (Middle Cenomanian), 30.3 km from Calabar.

REMARKS. This familiar species, discussed by Kennedy (1971: 30) and Juignet & Kennedy (1976: 65), is represented by a sole specimen from a horizon exposed 30.3 km from Calabar, marking the highest known occurrence of *Turrilites* in Nigeria. As mentioned above, individuals transitional between *T. costatus* and *T. acutus* occur lower in the Odukpani Formation. Successively younger populations, therefore, show a progressive reduction in rib development on the upper whorl sides.

Subfamily NOSTOCERATINAE Hyatt, 1894

Genus *PSEUDOXYBELOCERAS* Wright & Matsumoto, 1954

Subgenus *PARASOLENOCERAS* Collignon, 1969

TYPE SPECIES. *Parasolenoceras splendens* Collignon, 1969; by original designation.

REMARKS. Collignon (1969: 44) proposed the genus *Parasolenoceras* for specimens from the Lower Campanian of the Malagasy Republic showing a mode of coiling and ornament similar to that in *Solenoceras* Conrad, but which differ in the separation of the shafts of the shell. Subsequently Ward & Mallory (1977) introduced the subgenus *Pseudoxybeloceras* (*Cyphoceras*) (type species *Ancyloceras? lineatus* Gabb) for forms having a very similar coiling and ornamentation. *P. (Cyphoceras)* was defined by its relatively large shell coiled in a single plane, its ovoid whorl section, the presence of a single row of tubercles either side of the venter, and the separation of the shafts of the shell. Morphologically *P. (Cyphoceras)* is therefore intermediate between *P. (Pseudoxybeloceras)* Wright & Matsumoto and *Solenoceras*; Ward & Mallory (1977) considered it to be a subgenus of the former. In all respects *P. (Cyphoceras)* conforms with *Parasolenoceras*; Ward & Mallory (1977: 611) themselves considered the probability that its type species, *Parasolenoceras splendens* Collignon (1969: 44; pl. 530, figs 2087, 2088), belongs to *P. (Cyphoceras)*. As the name *Parasolenoceras* has



11a

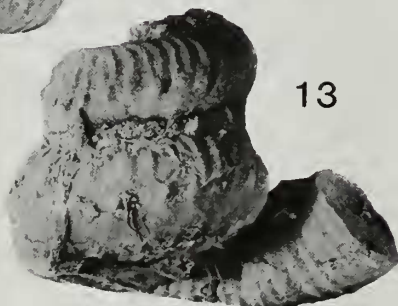


12

11b



10



13

priority over *P. (Cyphoceras)*, the latter name should be suppressed in its favour. The genus *Christophoceras* Collignon (1969: 47) differing from *Parasolenoceras* only in the periodic development of large inner ventrolateral tubercles, this too is here regarded as a synonym. As suggested by Ward & Mallory (1977), *Parasolenoceras* is probably best treated as a subgenus of *Pseudoxybeloceras*.

At present the following species can be referred to *Pseudoxybeloceras (Parasolenoceras)*: *Ancyloceras? lineatus* Gabb 1869 (see Matsumoto 1959: 162; pl. 40, figs 1a–d; pl. 41, figs 1a–c; Ward & Mallory 1977: 613; pl. 1, figs 1–7) and *Pseudoxybeloceras (Cyphoceras) nanaimoense* Ward & Mallory (1977: 615; pl. 2, figs 1–3; pl. 3, figs 1–3; text-fig. 3) from the Pacific Coast of North America; *Parasolenoceras splendens* Collignon (1969: 44; pl. 530, figs 2087, 2088) and *Christophoceras ramboulei* Collignon (1969: 47; pl. 531, fig. 2093) from the Malagasy Republic; *Pseudoxybeloceras bicostatum* Henderson (1970: 31; pl. 4, fig. 2) and *P. compressum* Henderson (1970: 31; pl. 4, fig. 4) from New Zealand; and an undescribed species from the Coniacian–Santonian of Hokkaido mentioned by Ward & Mallory (1977: 617). In addition *Hamites(?) clinensis* Adkins (1929: 208; pl. 6, figs 10, 11) from the Taylor Formation of Texas, dated by Young (1963) as Lower Campanian, may belong here.

The majority of previously-described species are of Campanian age though Henderson (1970: 31–32) reported *P. (Parasolenoceras) bicostatum* as having a possible range from Santonian to Maastrichtian. According to Ward & Mallory (1977), *P. (Parasolenoceras)* appeared in Coniacian or early Santonian times and gave rise to *Solenoceras* in the late Campanian. The fragment described below conforms well in all observable respects with *P. (Parasolenoceras)* but is of Upper Campanian age, making it amongst the youngest representatives of the subgenus. Typical diminutive *Solenoceras* occurs higher in Nigeria, being present in Lower Maastrichtian beds containing *Pachydiscus dossantosi* (Maury) and *Sphenodiscus* sp. at Akanu, some 90 km north-west of Calabar.

Pseudoxybeloceras (Parasolenoceras) aff. *splendens* Collignon, 1969
Fig. 11a, b

Compare: 1969 *Parasolenoceras splendens* Collignon: 44; pl. 530, figs 2087, 2088.

MATERIAL AND OCCURRENCE. A single specimen (C.83155) from the basal Nkporo Shale (Upper Campanian), about 36 km from Calabar.

DESCRIPTION. The material consists of a single fragment of what appears to be the distal part of the penultimate shaft of the shell. The last two shafts were not in contact. The whorl section is ovoid with the venter somewhat flattened. There are fairly dense ribs at the adapical end of the specimen, becoming coarser and more distant adorally. In most cases each rib bears a pair of tubercles, one each side of the venter, though occasionally one is absent or weakly developed. The tubercles become more prominent adorally. The ribs are indistinct between the tubercles, and along the dorsum where they are obvious only either side of two constrictions, one at the adoral end of the specimen and the other, shallower, 35 mm adapical of the first.

The suture is not displayed.

Fig. 8 *Turrilites (Turrilites) scheuchzerianus* Bosc. Odukpani Formation (Middle Cenomanian), 27.9 km from Calabar. C.82117, $\times 1$; note interruptions in ribs on lower half of whorl sides. See also Fig. 7.

Figs 9, 10 *Turrilites (Turrilites) costatus* Lamarck. Odukpani Formation (Middle Cenomanian), 28.3 km from Calabar. Fig. 9, C.83467, $\times 1$. Fig. 10, C.83470, $\times 1$.

Fig. 11a, b *Pseudoxybeloceras (Parasolenoceras)* aff. *splendens* Collignon. Lower Nkporo Shale (Upper Campanian), about 36 km from Calabar. C.83155, $\times 1$.

Figs 12, 13 *Didymoceras* aff. *hornbyense* (Whiteaves). Lower Nkporo Shale (Upper Campanian), about 36 km from Calabar. Fig. 12, C.85263, $\times 1$. Fig. 13, C.85264, $\times 1$. These spires probably represent the early whorls of specimens such as that shown in Fig. 14.

REMARKS. This specimen is less compressed than *Pseudoxybeloceras* (*Parasolenoceras*) *lineatum* (Gabb) (see Matsumoto 1959: 162; pl. 40, figs 1a–d; pl. 41, figs 1a–c; Ward & Mallory 1977: 613; pl. 1, figs 1–7) and much less so than *P. (Parasolenoceras) compressum* Henderson (1970: 31; pl. 4, fig. 4). The former species also shows occasional duplication of the tubercles. *P. (Parasolenoceras) bicostatum* Henderson (1970: 31; pl. 4, fig. 2) is smaller and with denser ribbing. *P. (Parasolenoceras) ramboulei* (Collignon 1969: 47) is quite different, showing periodic strengthened ribs with prominent inner and outer tubercle rows. *P. (Parasolenoceras) nanaimoense* (Ward & Mallory 1977: 615; pl. 2, figs 1–3; pl. 3, figs 1–3; text-fig. 3) shows periodic strong spines associated with two or three ribs. *P. (Parasolenoceras)? clinensis* (Adkins 1929: 208; pl. 6, figs 10, 11) has a less regular tubercle development, each being normally associated with a pair of ribs. This leaves *P. (Parasolenoceras) splendens* Collignon (1969: 44; pl. 530, figs 2087, 2088) as closest to the present material in shape and ornament, although it is of a somewhat older, Lower Campanian, age.

Genus *DIDYMO CERAS* Hyatt, 1894

TYPE SPECIES. *Ancyloceras? nebrascense* Meek & Hayden, 1856; by the original designation of Hyatt, 1894.

REMARKS. *Didymoceras* and related genera were discussed at length by Howarth (1965: 371–374). He concluded that *Cirroceras* Conrad is an unusable generic name which should be abandoned in favour of *Didymoceras* Hyatt, of which *Bostrychoceras* Hyatt was considered a synonym. *Nostoceras* Hyatt was retained as a relatively closely-defined genus. Although these conclusions were largely accepted by Matsumoto (1967: 339–341) and Lewy (1969: 110–111), the highly variable and intergradational nature of these heteromorph genera has led to a rather flexible treatment by authors. Klinger (1976: 63–64) placed all the above in the 'genus-group' *Didymoceras*. Although Jones (1963: 20) and Klinger (1976: 63–64) have pointed out that the distinction between *Nostoceras* and *Didymoceras* may well be entirely artificial, the two genera are separated here, following Howarth (1965). *Didymoceras* is therefore distinguished by its characteristically larger size, typically loosely coiled spire with the retroversal hook breaking away gradually, and its more complex ribbing with variably-developed tuberculation.

Didymoceras aff. *hornbyense* (Whiteaves, 1895)

Figs 12–14

- Compare: 1895 *Heteroceras hornbyense* Whiteaves: 316.
 1903 *Heteroceras hornbyense* Whiteaves; Whiteaves: 332; pl. 42, figs 1–4.
 1903 *Anisoceras cooperi* (Gabb); Whiteaves: 336; pl. 43, fig. 1.
 1952 *Nostoceras hornbyense* (Whiteaves) Usher: 103; pl. 27, figs 1, 2; pl. 31, fig. 23.
 1952 *Anisoceras cooperi* (Gabb); Usher: 107; pl. 29, fig. 1.
 1958 *Didymoceras whiteavesi* Anderson: 196.
 1963 *Didymoceras* aff. *D. hornbyense* (Whiteaves) Jones: 30; pl. 23, fig. 1.

MATERIAL AND OCCURRENCE. Six specimens (C.83144–5, C.83147–8, C.83152, UIN 499.1) from the basal Nkporo Shale (Upper Campanian), about 36 km from Calabar. In addition four other specimens (C.83146, C.83504, C.85263–4) from the same locality probably belong here.

DESCRIPTION. The specimens reach a large size. The whorls are more or less circular in cross section, with a diameter of about 30–40 mm at the retroversal point of the hook. Only the adoral part of the spire is known with certainty; here it appears to be loosely coiled with the retroversal hook breaking away gradually. The hook itself may be sharply retroversal with the two limbs almost in contact at the level of the aperture. The sutures are seen only in C.83147, in which the phragmocone includes the whole of the proximal limb of the retroversal hook.

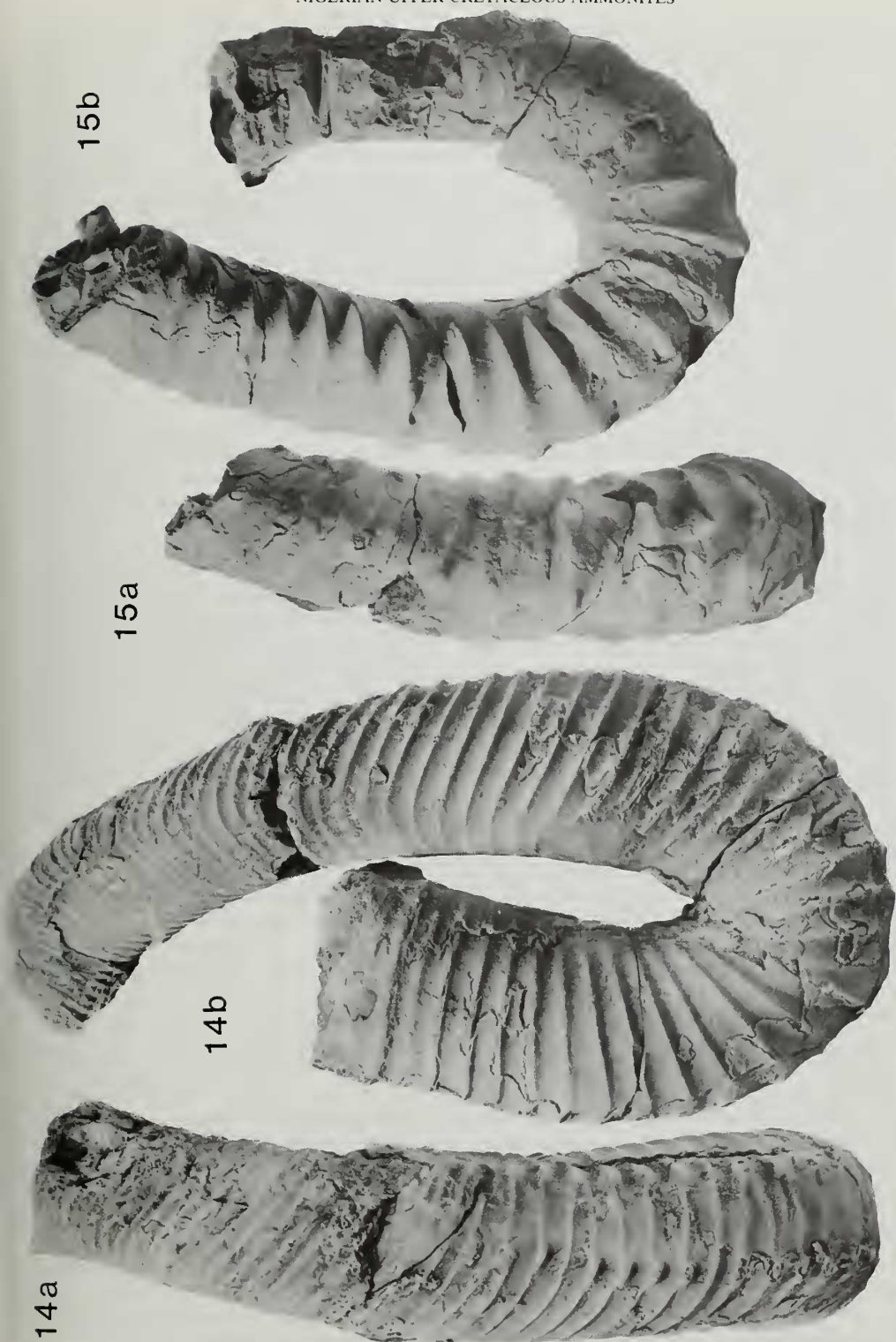


Fig. 14a, b *Didymoceras* aff. *hornbyense* (Whiteaves). Lower Nkporo Shale (Upper Campanian), about 36 km from Calabar. C.83144, $\times 0.75$.
See also Figs 12, 13.

Fig. 15a, b *Didymoceras* aff. *cheyennense* (Meek & Hayden). Lower Nkporo Shale (Upper Campanian), about 36 km from Calabar. C.83503, $\times 0.75$.

The last part of the spire and the early part of the retroversal hook bear fine, sporadically tuberculated ribs with an eccentric course. On the proximal limb of the hook the ribs become stronger, sharper and more distant: they die out along the dorsum. Typically, along the venter each rib bears a pair of weak to moderately well developed tubercles. The tubercles, at first on the lower surface of the whorl at the adoral end of the spire, gradually pass onto the periphery of the retroversal hook. Some ribs lack tubercles, occasionally some bifurcate, and in places some ribs zigzag between opposite and successive tubercles. On the distal limb of the hook each rib consistently carries a pair of tubercles though they lose a little strength adorally. At this stage the ribs show no tendency to zigzag between the tubercles. On the proximal limb of the hook the ribs are prorsiradiate, on the first part of the distal limb they are rursiradiate, and finally they become rectiradiate. The interspaces are wider than the ribs. The aperture is collared.

Occurring with these retroversal hooks are a number of incomplete spires (C.83146, C.83504, C.85263-4; Figs 12, 13), which are high with tight dextral or sinistral coiling. Their early whorls bear fine, dense, sharp curved ribs which become somewhat coarser and more distant adorally. Tubercles are developed on the majority of the ribs in two rows, one close to the middle of the whorl and the other lower down, close to the line of contact with the succeeding whorl. Between the tubercles the ribs are subdued or absent. Although none of these spires was found attached to the retroversal hook, it seems probable that they represent the early whorls of the material described above. One of the spires (C.85264, Fig. 13) shows the last whorl clearly breaking away towards the apex of the spire.

REMARKS. Jones (1963: 30-31) has reviewed the confused nomenclature of the nostoceratid ammonites of the Pacific Coast of North America. Of the four proposed names *Ammonites? cooperi* Gabb 1864, *Hamites vancouverensis* Gabb 1864, *Heteroceras hornbyense* Whiteaves 1895 and *H. perversum* Whiteaves 1895, only *H. hornbyense* can be adequately diagnosed. The precise relationships between these forms are unclear but *H. hornbyense* and the excellent specimen figured by Whiteaves (1903: pl. 43, fig. 1) as *Anisoceras cooperi* (Gabb) (= *Didymoceras whiteavesi* Anderson 1958: 196) may well be conspecific. The present specimens find their closest relationships with these North American forms, agreeing well in size and ornamental style. The retroversal hook figured by Jones (1963: pl. 23, fig. 1) as *Didymoceras* aff. *hornbyense* is particularly close in size, ornament and mode of coiling. The general features of the tuberculation are similar and the typical zigzagging of the ribs between the two rows of tubercles is shown by both. In general, however, the North American forms tend to show a less consistent tubercle development. Each tubercle is often associated with more than one rib, or is developed only on every second or third rib. In addition, the spire in *D. hornbyense* is rather broad and flat (Whiteaves 1903: pl. 42, figs 1-4; Usher 1952: pl. 27, figs 1, 2), unlike those described above in which the last whorl of the spire seems to break away in an adapical direction. Although no complete specimen has been found and a definite reconstruction of an entire shell cannot yet be produced, it seems possible that the present material had a mode of coiling similar to that in *Nostoceras* (*Anaklinoceras*) Stephenson (1941: 414), with the retroversal hook positioned above the spire, but this does not necessarily indicate a close relationship between *N. (Anaklinoceras)* and the present material. As Lewy (1969: 109-110) points out, in these heteromorphs the plane of the body chamber may form a great variety of angles with the axis of coiling of the spire. In size and ornament *N. (Anaklinoceras)* clearly has its affinities with *N. (Nostoceras)* (see Stephenson 1941), while in these respects the present material is closer to *Didymoceras*. A spire from the basal Nkporo Shale in Nigeria described by Reyment (1955: 13; pl. 1, fig. 3) as *Didymoceras hornbyense* (Whiteaves) is similar to those described here and may be conspecific.

As noted by Jones (1963: 31), the three species *Nostoceras mexicanum* Anderson (1958: 196; pl. 58, fig. 3), *Didymoceras kernense* Anderson (1958: 196; pl. 65, figs 1, 1a, 2) and *Exitoceras desertense* Anderson (1958: 202; pl. 66, figs 2, 2a) are all based on fragments and cannot be properly diagnosed. All show an ornament similar to that in *D. hornbyense*

and appear to be related to it. *Didymoceras fresnoense* Anderson (1958: 197; pl. 68, fig. 2) and *Exiteloceras bennisoni* Anderson (1958: 210; pl. 72, fig. 7) also belong in *Didymoceras*, but their precise relationships are unclear.

Didymoceras aff. *cheyennense* (Meek & Hayden, 1856)

Fig. 15a, b

Compare: 1856 *Ancyloceras?* *Cheyennense* Meek & Hayden: 71.

1876 *Heteroceras?* *Cheyennense* (Meek & Hayden); Meek: 483; pl. 21, figs 2a, 2b (with synonymy).

1973 *Didymoceras cheyennense* (Meek & Hayden); Gill & Cobban: 10, text-fig. 5c.

MATERIAL AND OCCURRENCE. A single specimen (C.83503) from the basal Nkporo Shale (Upper Campanian), about 36 km from Calabar.

DESCRIPTION. This large specimen consists only of the loosely coiled last part of the spire and the retroversal hook which breaks away gradually. The ornament consists of very coarse distant ribs each of which normally carries a pair of strong tubercles, although one or both may be absent especially on the proximal limb of the hook. The ribs sometimes bifurcate and may zigzag between the rows of tubercles, and there are a few intercalated ribs. The aperture is rather strongly collared.

REMARKS. In its coiling and general ornamental style the present specimen is essentially similar to the material described above as *Didymoceras* aff. *hornbyense*, differing mainly in its much coarser ornament. The two may represent varieties of a single species, although none of several unidentifiable heteromorph fragments also collected in the basal Nkporo Shale appears to be intermediate. For the present, therefore, this specimen is best compared with *Didymoceras cheyennense* (Meek & Hayden), a species proposed (Meek & Hayden 1856: 71) for a small fragment (see Meek 1876: pl. 21, figs 2a, 2b) and as such difficult to diagnose. Gill & Cobban (1973: text-fig. 5c), however, gave a restoration of a complete shell under this name. The holotype and this restoration agree with the Nigerian specimen in size and coarseness of the ribbing and the tuberculation on the retroversal hook. In *D. cheyennense*, however, each tubercle on the proximal limb of the retroversal hook is associated with two coarse ribs, while in the present specimen this part of the shell shows fine ribbing without tubercles.

Superfamily **DESMOCERATACEAE** Zittel, 1895

Family **DESMOCERATIDAE** Zittel, 1895

Subfamily **PUZOSIINAE** Spath, 1922

Genus **PUZOSIA** Bayle, 1878

Subgenus **ANAPUZOSIA** Matsumoto, 1954

TYPE SPECIES. *Puzosia buenaventura* Anderson, 1938; by the original designation of Matsumoto, 1954.

REMARKS. In *Puzosia* (*Anapuzosia*) the ribs appear at or near the umbilical margin, while in *P. (Puzosia)* Bayle they occur only on the ventral parts of the whorl sides. This subgenus is discussed by Matsumoto (1954), Renz (1972), Cooper (1978) and Wright & Kennedy (1981).

Puzosia (Anapuzosia) cf. *dibleyi* (Spath, 1922)

Fig. 16a, b

1855 *Ammonites austeni* Sharpe: 28; pl. 12, fig. 2 (only).

1922 *Austiniceras dibleyi* Spath: 127.

1931 *Puzosia matheroni* (d'Orbigny); Douvillé: 39; pl. 2, figs 5a, 5b (*non* d'Orbigny).

1951 *Austiniceras dibleyi* Spath; Wright & Wright: 19.

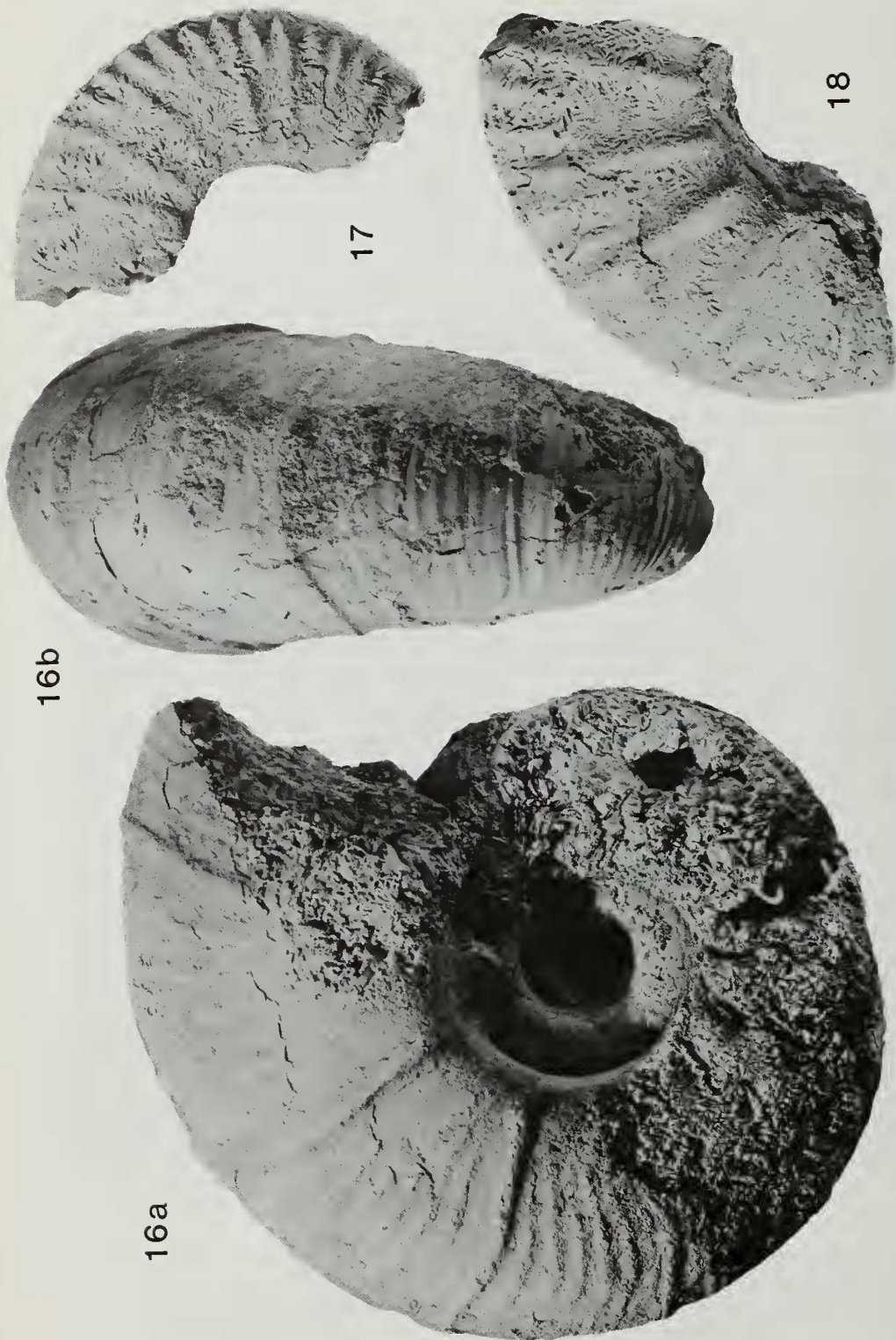


Fig. 16a, b *Puzosia* (*Anapuzosia*) cf. *dibleyi* (Spath). Odukpani Formation (Middle Cenomanian), 30.1 km from Calabar, C.83119, $\times 1$.
 Figs 17, 18 *Pachydiscus* (*Pachydiscus*) *dossantosi* (Maury). Upper Nkporo Shale (Lower Maastrichtian), 42 km from Calabar. Fig. 17, C.83206, $\times 1$. Fig. 18, C.83207, $\times 1$. See also Fig. 20.

- 1971 *Austiniceras dibleyi* Spath; Kennedy: 39; pl. 13, figs 1, 2; pl. 14, fig. 4.
 1978 *Puzosia (Anapuzosia) dibleyi* (Spath) Cooper: 78; figs 11A, 14B, 14C, 15B, 15C.
 1981 *Puzosia (Anapuzosia) dibleyi* (Spath); Wright & Kennedy: 19; pl. 1, fig. 2; pl. 2, fig. 4.

MATERIAL AND OCCURRENCE. A single specimen (C.83119) from the Odukpani Formation (Middle Cenomanian), 30.1 km from Calabar.

DESCRIPTION. The shell is moderately evolute, a little over half the previous whorl being covered. The whorls are moderately compressed with broadly rounded flanks converging upon the rounded venter. There are nine major sinuous ribs on the last preserved whorl originating at the umbilical shoulder. These ribs are associated with constrictions on the internal mould. Between the major ribs are five to nine intercalated, less pronounced ribs, some of which arise just outside the umbilical shoulder, others more ventrally on the flank.

REMARKS. This specimen agrees closely with *Puzosia (Anapuzosia) dibleyi* (Spath) in gross morphology and ornamentation. An Angolan individual figured by Kennedy (1971: pl. 13, fig. 1) is an almost exact match but is a little more compressed. The English Chalk material (Kennedy 1971: pl. 13, fig. 2; pl. 14, fig. 4; Wright & Kennedy 1981: pl. 1, fig. 2; pl. 2, fig. 2) is crushed, making comparison in this respect difficult. Hitherto *P. (A.) dibleyi* has been known only from southern England (see above) and Angola (Douvillé 1931, Cooper 1978) and in both places it characterizes beds of uppermost Cenomanian age. It is therefore typical of a higher horizon than the Nigerian specimen.

The Albian species *P. (Anapuzosia) multicostata* Renz (1972: 707; pl. 2, figs 1, 2; pl. 3, fig. 1; pl. 9, fig. 4), *P. (A.) saintoursi* Collignon (1963: pl. 263, fig. 1150; pl. 266, fig. 1157) and *P. (A.) colusaensis* (Anderson 1902: 96; pl. 5, figs 128, 129; pl. 10, fig. 200) all have more numerous, finer, denser intercalated ribs and typically show fewer major ribs.

Family **PACHYDISCIDAE** Spath, 1922

Genus **PACHYDISCUS** Zittel, 1884

Subgenus **PACHYDISCUS** Zittel, 1884

TYPE SPECIES. *Ammonites neubergicus* Hauer, 1858; by the subsequent designation of Grossouvre, 1894.

Pachydiscus (Pachydiscus) egertoni (Forbes, 1846) Fig. 19a, b

- 1846 *Ammonites Egertoni* Forbes: 108; pl. 9, fig. 1.
 1864 *Ammonites egertonianus* Forbes; Stoliczka: 104; pl. 53.
 1898 *Pachydiscus egertonianus* (Forbes) Kossmat: 159; pl. 21, figs 4a-c.
 ? 1955 *Pachydiscus* aff. *stallauensis* Imkeller; Reymont: 17 (*non* Imkeller).
 ? 1957 *Pachydiscus* aff. *stallauensis* Imkeller; Reymont: 63; pl. 11, figs 2a, 2b (*non* Imkeller).
 1959 *Pachydiscus egertoni* (Forbes); Matsumoto: 42, text-fig. 17.

MATERIAL AND OCCURRENCE. Two specimens (C.83140, C.83500) from the basal Nkporo Shale (Upper Campanian), about 36 km from Calabar.

DIMENSIONS.	D	Wb	Wh	U
C.83500	102	33 (32.2)	41 (40)	31 (30.4)
	72	24 (33.3)	31 (43)	20 (28)
	51	18 (35.3)	21 (41)	13 (25.8)

DESCRIPTION. The phragmocone reaches a diameter of at least 150 mm. The whorls are compressed, whorl height increasing a little more rapidly than whorl breadth during ontogeny, the flanks being flattened and the venter rounded. The shell is moderately evolute, a little over half the previous whorl being covered at the largest diameter seen (150 mm). The umbilicus widens slightly during ontogeny. The ornament consists of narrow rounded ribs which are pronounced just outside the umbilical shoulder but which fade on the

ventral part of the whorl and are missing over the venter, at least at larger diameters. As growth proceeds they become more distant, only eight being present on the last preserved whorl in C.83500. The strength of the ribs does not increase appreciably during ontogeny and hence the inner whorls appear more coarsely ornamented than the outer.

REMARKS. The present material is closely comparable to *Pachydiscus* (*P.*) *egertoni* (Forbes). The lectotype (C.51038, see Forbes 1846: pl. 9, fig. 1; sel. Matsumoto 1959: 42, text-fig. 17) differs only in its slightly greater whorl compression and rather more prominent umbilical bullae. *P.* (*P.*) *neubergicus* (Hauer 1858: 12; pl. 2, figs 1, 2; pl. 3, figs 1, 2) is similar but retains minor ventral ribbing in the later stages and shows major ribs continuous over the venter. The latter are, however, most pronounced on the dorsal half of the whorl as in *P.* (*P.*) *egertoni*.

Part of a juvenile whorl described by Reyment (1955: 17; 1957: 63; pl. 11, figs 2a, 2b), from a horizon of the same age near Afikpo to the north-west of Calabar, is probably conspecific with the present material. Reyment placed this individual in *Pachydiscus* aff. *stallauensis* Imkeller. Its ribbing is similar in style to that in the present material, although both major and minor ribs are present and its whorl section is a little less compressed. These, however, are probably juvenile features, being similar to those of the early stages in *P.* (*P.*) *egertoni* where minor ventral ribs are present in the lectotype and in a specimen described by Kossmat (1898: 159; pl. 21, figs 4a–c). The adult whorls in *P.* (*P.*) *stallauensis* differ from those in the present material in showing denser but more feeble ribs (see Imkeller 1901: pl. 3, fig. 5).

***Pachydiscus* (*Pachydiscus*) *dossantosi* (Maury, 1930)**

Figs 17, 18, 20

1930 *Parapachydiscus dossantosi* Maury: 136; pl. 16, fig. 1; pl. 17, figs 1, 2.

?1944 *Parapachydiscus* sp. Olsson: 107; pl. 16, fig. 1.

MATERIAL AND OCCURRENCE. Twenty-five specimens (C.82125–6, C.82151–4, C.82176, C.83205–8, C.83506–7, C.85269, UIN 437.1–11) from the upper Nkporo Shale (Lower Maastrichtian), 42 km from Calabar.

DESCRIPTION. The shell reaches a diameter of at least 220 mm and is fairly evolute, about half the previous whorl being covered. In the early stages the whorls are only a little higher than broad with convexly rounded flanks and a rounded venter. Whorl height increases more rapidly than whorl breadth so that in the later stages the whorls are distinctly compressed with rather flattened flanks and a broadly arched venter.

There are approximately 42 ribs per whorl in the middle stages. Most are short, extending over the ventral third to half of the whorl, and are concealed by the succeeding whorl. Every second to fourth rib is extended to the umbilical shoulder. These major ribs attain their greatest development on the dorsal third of the flank and are sometimes very faint, almost interrupted, in the middle part of the flank. On internal moulds the ribs are interrupted to a greater or lesser extent along the venter by a siphonal groove. Towards adulthood the intercalated ventral ribs become fewer, from generally two or three to only one or two.

REMARKS. In general morphology this material is close to certain of the north-west European Lower Maastrichtian pachydiscids, particularly *Pachydiscus* (*P.*) *gollevillensis* (d'Orbigny). In that species, however, the ornament usually consists of discrete umbilical bullae and ventral ribs which are finer and more numerous than in the Nigerian specimens. In some examples the umbilical bullae may extend across the flanks and join the ventral ribs (see, for example, Grossouvre 1894: pl. 29, figs 4a, 4b), such individuals coming to resemble the

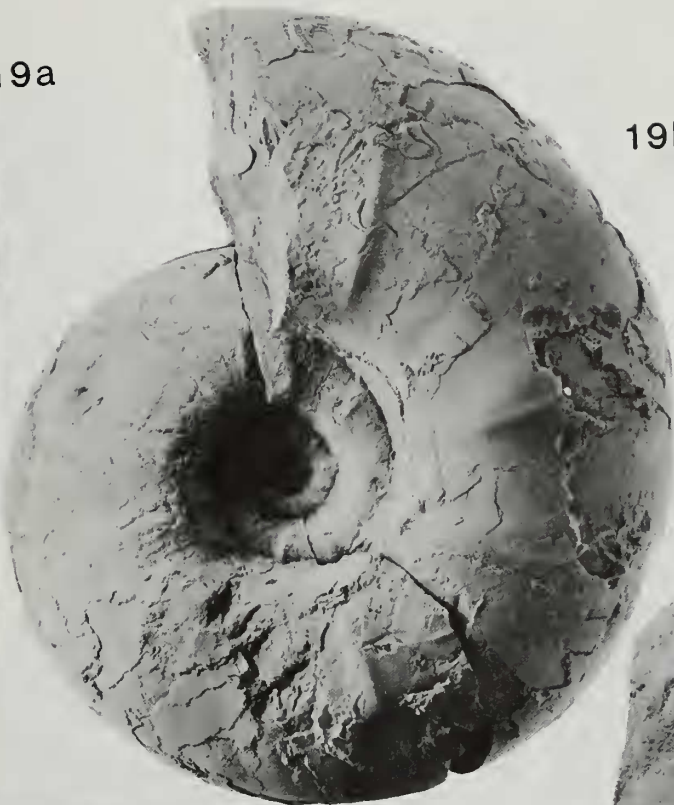
Fig. 19a, b *Pachydiscus* (*Pachydiscus*) *egertoni* (Forbes). Lower Nkporo Shale (Upper Campanian), about 36 km from Calabar. C.83500, $\times 0.75$.

Fig. 20a, b *Pachydiscus* (*Pachydiscus*) *dossantosi* (Maury). Upper Nkporo Shale (Lower Maastrichtian), 42 km from Calabar. C.85269, $\times 1$. See also Figs 17, 18.

19a



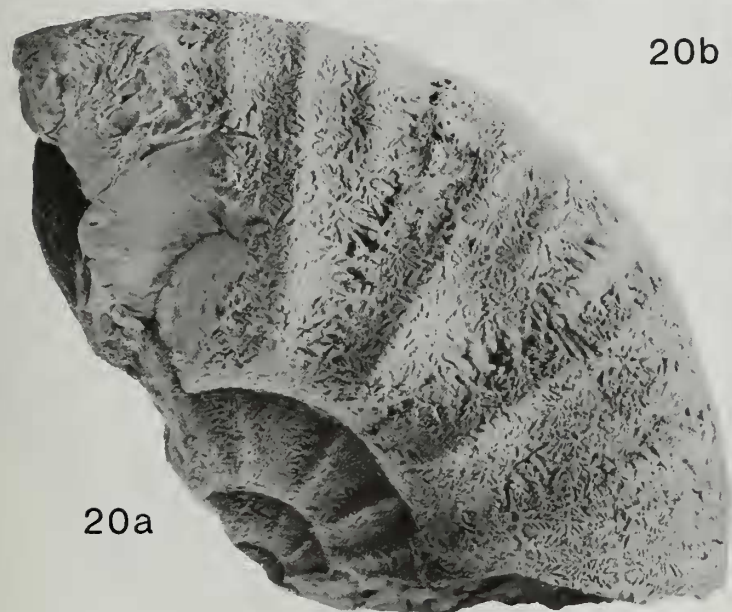
19b



20b



20a



present material. A similar trait exists in specimens from the United States related to *P. (P.) gollevillensis* (Young 1963: pl. 14, figs 2, 3). *P. (P.) neubergicus* (Hauer) may also show this type of ornament (Hauer 1858: pl. 2, figs 1, 2; Grossouvre 1894: pl. 26, fig. 3a; pl. 38, fig. 3), but has a more compressed shell, while *P. (P.) jacquoti* Seunes (1890: pl. 2, figs 1–3; pl. 3, figs 4a, 4b), also with this ornamental style, has rather inflated whorls.

Most closely comparable with the Nigerian material is *P. (P.) dossantosi* (Maury 1930: 136; pl. 16, fig. 1; pl. 17, figs 1, 2) from eastern Brazil. This species has an overall morphology and ornament of precisely the same type as the present material, and also shows a reduction in the number of intercalated ribs towards adulthood. Two other Brazilian species, *P. (P.) gettyi* (Maury 1930: 138; pl. 14, figs 1, 2) and *P. (P.) endymion* (Maury 1930: 156; pl. 32), are close to *P. (P.) dossantosi* and may be synonyms. A *Pachydiscus* from Peru described by Olsson (1944: 107; pl. 16, fig. 7) is also very similar to *P. (P.) dossantosi*.

Superfamily ACANTHOCERATACEAE Grossouvre, 1894

Family FORBESICERATIDAE Wright, 1952

Genus *FORBESICERAS* Kossmat, 1897

TYPE SPECIES. *Ammonites largilliertianus* d'Orbigny, 1841; by the subsequent designation of Diener, 1925.

Forbesiceras subobtectum (Stoliczka, 1864)

Fig. 21a, b

1864 *Ammonites subobtectus* Stoliczka: 96; pl. 49, figs 2, 2a, 2b.

1964 *Forbesiceras subobtectum* (Stoliczka) Collignon: 62; pl. 335, fig. 1501.

MATERIAL AND OCCURRENCE. A single specimen (C.83430) from the Odukpani Formation (Middle Cenomanian), 27.9 km from Calabar.

REMARKS. This specimen reaches a diameter of some 180 mm. The outer whorl shows a broad venter but is otherwise poorly preserved. Between diameters of about 60–80 mm the specimen shows an ornament typical of this species (see Stoliczka 1864: pl. 49, fig. 2), with a broad venter bordered on each side by a row of coarse tubercles with fine transverse ribbing between. The dorsal part of the flank bears pronounced prorsiradiate ribs terminating in coarse nodes in the mid-flank region, while there are coarse moderately rursiradiate ribs on the ventral third of the flanks.

Forbesiceras obtectum (Sharpe, 1853)

Figs 22–25, 29

1853 *Ammonites obtectus* Sharpe: 20; pl. 7, figs 4a–c.

1907 *Forbesiceras obtectum* (Sharpe) Pervinquière: 108; pl. 6, figs 7–11.

1928 *Forbesiceras obtectum* (Sharpe); Collignon: pl. 2, figs 13, 13a.

1929 *Forbesiceras obtectum* (Sharpe); Collignon: 27.

1940 *Forbesiceras obtectum* (Sharpe); Fabre: 222; pl. 5, fig. 14.

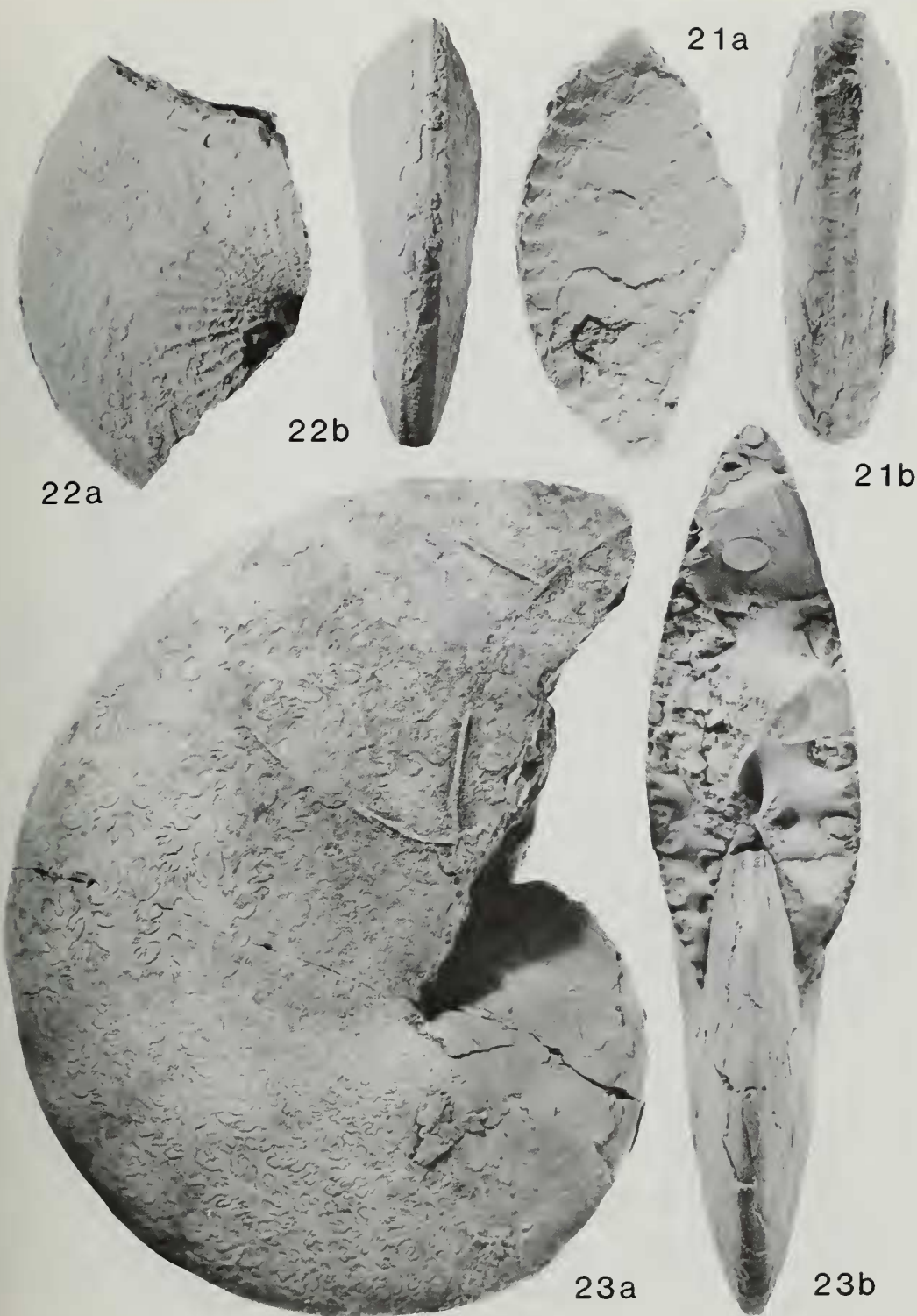
1971 *Forbesiceras obtectum* (Sharpe); Kennedy: 47; pl. 9, figs 3a, 3b; pl. 16, fig. 3; pl. 46, fig. 3 (with synonymy).

1973 *Forbesiceras obtectum* (Sharpe); Cooper: 48; figs 5, 6A, 6B.

1976 *Forbesiceras obtectum* (Sharpe); Juignet & Kennedy: 82; pl. 5, figs 9a, 9b, 10a, 10b; pl. 6, figs 2a, 2b, 3a–c, 4, 5.

Fig. 21a, b *Forbesiceras subobtectum* (Stoliczka). Odukpani Formation (Middle Cenomanian), 27.9 km from Calabar. C.83430, $\times 1$.

Figs 22, 23 *Forbesiceras obtectum* (Sharpe). Odukpani Formation (Middle Cenomanian). Fig. 22a, b, from an uncertain locality, Calabar–Ikot Ekpene road. C.82148, $\times 1$. Fig. 23a, b, 29.3 km from Calabar. C.83107, $\times 0.65$. See also Figs 24, 25, 29.



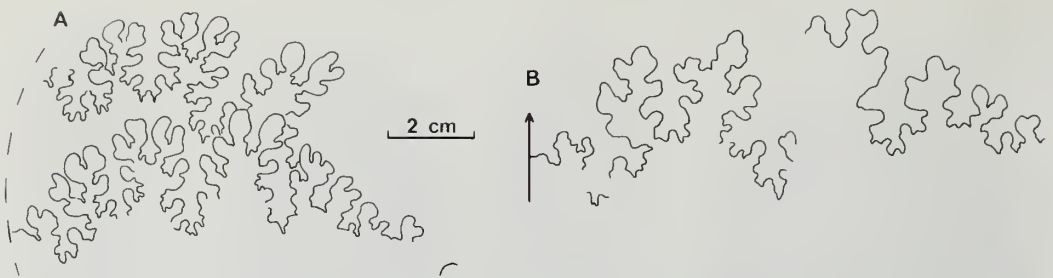


Fig. 24 Sutures in *Forbesiceras obtectum* (Sharpe). A, C.83107 at diameter of 165 mm; B, C.83549.

MATERIAL AND OCCURRENCE. Seven specimens (C.82112, C.82114, C.82148–9, C.83107, C.83476, C.83549) from the Odukpani Formation (Middle Cenomanian) can be definitely referred to this species. C.83107 is from a horizon exposed 29.3 km from Calabar, C.83476 and C.83549 from 30.3 km from Calabar: the remainder cannot be precisely localized. In addition two fragmentary specimens (C.83475, UIN 474.1) from 30.1 km from Calabar probably belong in this species.

DIMENSIONS.	D	Wb	Wh	U
C.83107	205	46 (22.4)	125 (61)	—
	155	36 (23)	100 (64.5)	—
	92	20 (22)	55 (60)	—

DESCRIPTION. The present material falls into two groups. Up to a diameter of some 80 mm development in both groups is similar, the ornament consisting of prorsiradiate ribs on the dorsal part of the flanks terminating in a row of bullate swellings or discrete tubercles in the middle of the flanks, while the ventral half of the flanks bear rursiradiate ribs terminating in fine clavate tubercles at the ventrolateral shoulder. The venter is narrowly fastigiate with dense nodate to bullate siphonal tubercles. The ornament at this stage is usually fairly pronounced.

At diameters in excess of 80 mm, however, development in the two groups differs markedly. The first group, represented by C.82112 (Fig. 29a, b), reaches full adult size at a diameter of some 110 mm, at which stage the sutures are simplified and approximated and the umbilicus is egressing, and the ornament is reduced in strength. The ribs are continuous from umbilicus to venter and are only slightly prorsiradiate on the dorsal part of the flanks and only slightly rursiradiate on the ventral part. The venter becomes broadly rounded with only a slight keel evident on the internal mould. The last third of the final whorl on this specimen is body chamber. It bears a broad deep pre-oral constriction swept forwards on the dorsal part of the flank and backwards on the ventral part.

The second group is more fully represented in the present collection (C.83107, C.83476, C.83549 and probably C.83475 and UIN 474.1; Figs 23a, b, 25a, b). Its members attain a very large size, the diameter of the phragmocone exceeding 250 mm. The strength of the ornament is also reduced during growth. At diameters of about 100 mm it is possible to make out weak prorsiradiate ribs on the dorsal part of the flanks and discontinuous rursiradiate ribs on the ventral part. At larger diameters, however, at least on internal moulds, the flanks appear perfectly smooth. At a diameter of 100 mm the venter appears narrowly fastigiate

Fig. 25a, b *Forbesiceras obtectum* (Sharpe). Odukpani Formation (Middle Cenomanian), 30.3 km from Calabar. C.83476, $\times 0.65$. See also Figs 22–24, 29.

Figs 26–28 *Sharpeiceras laticlavium nigeriense* subsp. nov. Odukpani Formation (Lower Cenomanian), Calabar–Akamkpa road, 1.5 km north of junction with Calabar–Ikot Ekpene road. Fig. 26, paratype C.83542, $\times 1$. Fig. 27a, b, **holotype** C.83544, $\times 1$. Fig. 28a, b, paratype C.83545, $\times 1$. See also Fig. 31.

25a



25b



26



27a



27b



28a



28b



where the test is preserved, though on internal moulds it is sharply rounded at this and larger diameters. The suture pattern is variable in its details (Fig. 24). The saddles may become highly elongated with phylloid endings. The sutures may be crowded and overlapped, even at intermediate diameters.

REMARKS. The two groups of this form described above appear to represent the microconch and macroconch of a dimorphic species. The large individuals of the second group conform closely with huge specimens which Cooper (1973: 48–49) found to be common in the Middle Cenomanian near Novo Redondo, Angola. *Forbesiceras obiectum* also occurs in southern England but is rare. Juignet & Kennedy (1976: 82–83) divided this material into two groups. The first, exemplified by the specimens figured by Kennedy (1971: pl. 16, fig. 3; pl. 46, fig. 3), shows finely ornamented, almost smooth adult whorls. These forms are comparable to the large Nigerian specimens. The second group, exemplified by the specimen figured by Kennedy (1971: pl. 5, figs 9a, 9b), contains forms grossly ornamented to a large size with a broad venter carrying coarse ventrolateral and siphonal tubercles. Intermediate forms from the low Middle Cenomanian Rouen fossil bed in north-west France were described by Juignet & Kennedy (1976: pl. 5, figs 10a, 10b; pl. 6, figs 2a, 2b). Nothing in the Nigerian collection is closely comparable to Juignet & Kennedy's second group, which appears to be intermediate between *F. subobtectum* (Stoliczka) and *F. obiectum*. In the Odukpani Formation horizons known to contain *F. obiectum* lie above that with *F. subobtectum*. It is possible that reduction in strength of the ornament and breadth of the venter are stratigraphic trends in this group of *Forbesiceras*. The differences between the two Nigerian groups of *F. obiectum* described here, however, seem to be due to dimorphism.

Two large specimens of *Forbesiceras* (C.83548, UIN 475.1), both reaching a diameter of some 250 mm, come from the lower part of the Odukpani Formation at 25.8 km from Calabar, and consist only of the outer whorl. They resemble the large specimens of *F. obiectum* described above, but in the absence of the inner whorls cannot be identified to species level. Species of *Forbesiceras* from various levels in the Cenomanian are closely alike at large diameters, showing smooth compressed whorls with a sharply rounded venter. *F. largilliertianum* (d'Orbigny), which occurs in the Lower Cenomanian of southern England (Kennedy & Hancock 1978), has such an adult morphology (see Sharpe 1853: pl. 7, figs 1a, 1b), as does *F. conlini* Stephenson (1952: 205; pl. 56, fig. 1; pl. 57, figs 2–6) from the Middle Cenomanian of Texas. Material from the late Cenomanian of western France referred to *F. aff. largilliertianum* by Kennedy, Juignet & Hancock (1981: 39; figs 7, 10A) is also of this form at large sizes.

Family ACANTHOCERATIDAE Grossouvre, 1894

Subfamily MANTELLICERATINAE Hyatt, 1903

Genus *SHARPEICERAS* Hyatt, 1903

TYPE SPECIES. *Ammonites laticlavus* Sharpe, 1855; by original designation of Hyatt, 1903.

Sharpeiceras laticlavium (Sharpe) *nigeriense* subsp. nov.

Figs 26–28, 31

HOLOTYPE. C.83544, showing the juvenile whorls (Fig. 27a,b). From the Odukpani Formation (Lower Cenomanian), cutting on the Calabar–Akamkpa road, 1.5 km north of the junction with the Calabar–Ikot Ekpene road.

PARATYPES. C.83542–3, C.83545, UIN 500.1, all from the same locality as the holotype.

NAME. From Nigeria.

DIAGNOSIS. *Sharpeiceras* with distant ribs and spinose inner and outer ventrolateral tubercles in the early stages, but with closely-spaced ribbing and subdued tuberculation in the middle stages. Both major and minor ribs present throughout.



Fig. 29a, b *Forbesiceras obtectum* (Sharpe). Odukpani Formation (Middle Cenomanian), from an uncertain locality, Calabar-Ikot Ekpene road. C.82112, an adult microconch, $\times 1$. See also Figs 22–25.

Fig. 30a, b *Acompsoceras calabarensense* sp. nov. Odukpani Formation (Lower Cenomanian), Calabar-Akamkpa road, 1.5 km north of junction with Calabar-Ikot Ekpene road. Paratype C.83553, $\times 1$. See also Fig. 32.

Fig. 31a, b *Sharpeiceras laticlavium nigeriense* subsp. nov. Odukpani Formation (Lower Cenomanian), Calabar-Akamkpa road, 1.5 km north of junction with Calabar-Ikot Ekpene road. Paratype C.83543, $\times 1$. See also Figs 26–28.

DESCRIPTION. The shell is moderately evolute with high, flattened whorl sides. The largest specimen (C.83542), fully septate, attains a diameter of some 110 mm.

At a diameter of 15 mm there are 15 low, narrow, rounded ribs in each whorl. Each rib bears prominent inner and outer ventrolateral tubercles. On the flank the ribs are alternately long and short. The former terminate in low bullate umbilical tubercles, the latter die out in the middle part of the flank.

In the complete whorl between diameters of 22 and 55 mm there are 18 rows of pronounced spinose inner and outer ventrolateral tubercles. Ten of these rows are associated with long, narrow, rounded ribs which cross the flank and terminate in well-developed conical umbilical tubercles. The remainder are borne upon shorter ribs which terminate in the middle or dorsal half of the flank. At a diameter of 30 mm mid-lateral tubercles appear. At first they are close to the umbilical shoulder, but they gradually migrate ventrally taking up a position just dorsal of the middle of the flank. The short ribs generally lack mid-lateral tubercles. In the early stages the whorls are markedly higher than broad, with a rather narrow venter.

As growth proceeds the ventrolateral and umbilical tubercles become subdued while rib density increases markedly. In the half whorl between diameters of about 65 and 110 mm in C.83542 there are approximately 18 rounded ribs of width equal to that of the interspaces. Most of these ribs arise at a variably pronounced, bullate or pointed, umbilical tubercle and bear a prominent mid-lateral tubercle and weaker inner and outer ventrolateral tubercles which may tend to fuse into a bullate swelling crossing the ventrolateral shoulder. Intercalated ribs, also bearing inner and outer ventrolateral tubercles, are present. Some die out ventral of the mid-lateral tubercles, others bear a subdued mid-lateral tubercle and terminate just dorsal of the umbilical shoulder. Occasionally, ribs bifurcate at the mid-lateral tubercles. At this stage whorl height exceeds whorl breadth but the venter is wide and flat, being bordered by sloping ventrolateral shoulders.

The suture is complex with E and L deep and highly subdivided while the saddles exhibit subphylloid endings.

REMARKS. This *Sharpeiceras* has a distinctive ontogenetic development and is easily distinguished from most previously described species. *S. schlueteri* (Schlüter 1871: 18; pl. 7, figs 4-9; Hyatt 1903: 111) is more evolute with coarser ribbing in the middle stages. *S. vohipalense* Collignon (1964: 104; pl. 354, fig. 1565) also shows stronger ribbing in the middle stages, at which the inner ventrolateral tubercles become exaggerated rather than subdued. *S. occidentale* Benavides-Cáceres (1956: 465; pl. 54, figs 5, 6) is more compressed in its later stages with a coarser decoration. *S. congo* Matsumoto, Muramoto & Takahashi (1969: 261; pl. 29, fig. 1; pl. 30, fig. 1) has coarse distant ribbing throughout ontogeny with massive tuberculation developing in the later stages. *S. florencae* Spath (1925: 198; pl. 37; Kennedy 1971: 67; pl. 25, fig. 2) has a more depressed whorl section and coarser ornament in the middle stages. *S. tlahualiloense* (Kellum & Mintz 1962: 276; pl. 6, fig. 1; pl. 7, figs 1, 2; pl. 8, fig. 1) is similar to *S. florencae* and may be a synonym (see also Juignet & Kennedy 1976: 100). *S. corroyi* (Fabre 1940: pl. 7, figs 5, 6) is more evolute and compressed with a rounded venter and broad ribbing. *S. piveteaui* Collignon (1928-29: 37; pl. 3, figs 18, 18a) is a nucleus of less than 20 mm diameter impossible to compare with other material. *S. falloti* (Collignon 1931: 41; pl. 4, figs 9-12) is also based on juvenile specimens. They resemble the early whorls in *S. laticlavium nigeriense* although they seem to have a somewhat greater rib density at diameters of less than 20 mm. The two may be closely related but ignorance of the later whorls makes detailed comparison impossible. Undoubtedly close to the present material is *S. laticlavium* (Sharpe), of which *S. goliath* Haas (1942: 7, fig. 7) is a synonym (see Kennedy 1971: 66; Cooper 1978a: 6). The holotype (Sharpe 1855: pl. 14, figs 1a, 1b; Kennedy 1971: pl. 27, figs 1a-c) has a very similar gross morphology and ornament in its middle stages. Its ventrolateral tubercles lack the early spinosity of those in the Nigerian material but this is probably an effect of preservation. The ornament of the early whorls is unclear in the holotype, as it is in conspecific French material described by Juignet &

Kennedy (1976: 99; pl. 10, figs 1, 2). Rib density here, however, seems to be greater than in the Nigerian form, this being the major difference between the two. In view of their overall similarity, however, they are separated here at the subspecific level only. *S. laticlavium* var. *indica* (Kossmat 1895: 103; pl. 10, figs 5, 6) also has a similar ontogenetic development, but again the ribs are more closely spaced in the early stages and less crowded at diameters of 100 mm or so, at which stage the whorls are more compressed. In *S. laticlavium* var. *mexicanum* Böse (1927: 253; pl. 10, fig. 6; pl. 11, fig. 1) the ribs are said to spring in pairs from the umbilical tubercles, this form also being rather highly compressed.

Genus *ACOMPSOCERAS* Hyatt, 1903

TYPE SPECIES. *Ammonites bochumensis* Schlüter 1871; by the original designation of Hyatt, 1903.

Acompsoceras calabarensis sp. nov.

Figs 30, 32

HOLOTYPE. C.85250, about half a whorl (Fig. 32a, b). From the Odukpani Formation (Lower Cenomanian), cutting on the Calabar-Akamkpa road, 1.5 km north of the junction with the Calabar-Ikot Ekpeni road.

PARATYPES. C.83552-3, C.85249, C.85251, all from the same locality as the holotype.

NAME. After the town of Calabar, close to the locality of the type material.

DIAGNOSIS. *Acompsoceras* with coarse, alternately long and short ribs. Umbilical tubercles large and bullate, inner ventrolateral tubercles prominent and rounded, outer ventrolateral tubercles markedly clavate. Mid-lateral tubercles absent.

DESCRIPTION. The holotype consists of approximately half a whorl with a diameter of 100 mm. It displays 11 broad rounded ribs, alternately long and short. The long ribs carry pronounced, highly bullate umbilical tubercles, prominent rounded inner ventrolateral tubercles and markedly clavate outer ventrolateral tubercles. The short ribs lack, or display only weakly-developed, umbilical tubercles. The venter is narrow and flat. There are no mid-lateral tubercles. The whorls in the holotype are rather compressed with flattened flanks converging slightly ventrally. A smaller specimen (C.83553, Fig. 30a, b) shows a broader pentagonal whorl section at a diameter of some 40 mm. At this stage the ribs are narrower and sharper.

REMARKS. This *Acompsoceras* is easily distinguished from most previously described species by its very coarse ornament. *A. pseudosarthense* Collignon (1964: 108; pl. 356, fig. 1568), *A. tenue* Collignon (1964: 110; pl. 357, figs 1572, 1573), *A. catzigrasae* (Collignon (1964: 112; pl. 358, fig. 1577), *A. sahnii* Collignon (1964: 111; pl. 358, figs 1575, 1576) and *A. viotti* Collignon (1966: 26; pl. 16, fig. 1) all have finer, denser, ribbing. *A. antsatramahaveloense* Collignon (1964: 109; pl. 357, fig. 1571) has broader more rectangular whorls. *A. essendiense* (Schlüter 1871: 3; pl. 1, figs 5-7; pl. 2, fig. 2) has a very feeble umbilical and ventrolateral ornament which disappears later in ontogeny. *A. renevieri* (Sharpe 1857: 44; pl. 20, figs 2a-c; Kennedy 1971: 68; pl. 30, figs 1a-c) lacks well-developed ribbing and inner ventrolateral tubercles. A specimen from the Odukpani Formation referred by Reymont (1957: 60; pl. 8, figs 3a, 3b) to *A. subwaterloti* Venzo shows broader, flatter ribbing and sharper ventrolateral tubercles. It displays mid-lateral tubercles but lacks inner ventrolateral tubercles. The same style of ribbing is shown by the holotype of *A. subwaterloti* (Venzo 1936: 87; pl. 7, figs 11a, 11b). It also lacks inner ventrolateral tubercles, but this is a very small specimen making detailed comparison difficult. Closest to the present material is *A. sarthense* (Guéranger 1867: 5; pl. 4, fig. 1; pl. 8, fig. 2), which has a similar gross morphology and only slightly finer ornament (see Kennedy 1971: 67; pl. 26, fig. 3; pl. 29, figs 1a-c). This species, however, has mid-lateral tubercles and its umbilical tubercles are far less swollen and bullate than in *A. calabarensis*.

Acompsoceras aff. *renevieri* (Sharpe, 1857)

Fig. 33a, b

Compare: 1857 *Ammonites renevieri* Sharpe: 44; pl. 20, figs 2a–c.1971 *Acompsoceras renevieri* (Sharpe); Kennedy: 68; pl. 30, figs 1a–c (with synonymy).

MATERIAL AND OCCURRENCE. Four specimens (C.83498, C.85248, UIN 482.1–2) from the Odukpani Formation (Lower? Cenomanian), cutting on the Calabar–Akamkpa road, 1 km north of the junction with the Calabar–Ikot Ekpene road.

REMARKS. These specimens, which reach a large size, show sparse, broad, bulge-like ribs on the dorsal half of the flanks. The venter is bordered by numerous, fine, clavate ventrolateral tubercles. *Acompsoceras renevieri* (Sharpe) (see Kennedy 1971: 68; pl. 30, figs 1a–c) has a very similar ornament, although it has fewer and coarser ventrolateral tubercles. The two are closely related, but better material is needed to clarify the taxonomic status of the Nigerian form.

Genus *PSEUDOCALYCOCERAS* Thomel, 1969

TYPE SPECIES. *Ammonites harpax* Stoliczka, 1865; by the original designation of Thomel, 1969.

Pseudocalycoceras cf. *haughi* (Pervinqui re, 1907)

Fig. 34a, b

1907 *Acanthoceras haughi* Pervinqui re: 270; pl. 14, figs 1a, 1b.1972 *Pseudocalycoceras* (*Haughiceras*) *haughi* (Pervinqui re) Thomel: 97; pl. 131, figs 7, 8 (with synonymy).1981 *Pseudocalycoceras haughi* (Pervinqui re); Kennedy, Juignet & Hancock: 48.

MATERIAL AND OCCURRENCE. A single specimen (C.82111) from an uncertain horizon in the Odukpani Formation (Upper Cenomanian), Calabar–Ikot Ekpene road.

DESCRIPTION. This specimen consists of just over one-third of a whorl. It has a pentagonal costal section while intercostally the flanks and venter are broadly rounded. The whorl is a little broader than high, the greatest intercostal breadth being at the level of the umbilical tubercle. There are seven narrow, rounded major ribs and three minor ribs on this specimen, the latter not reaching the umbilical shoulder. At the adapical end of the specimen each major rib carries a pair of unevenly developed knob-like umbilical tubercles, sometimes highly effaced, a pair of inner and outer ventrolateral tubercles and a weakly developed siphonal tubercle. All the tubercles are bullate. On the flanks the ribs are rursiradial, they are bent forwards between the inner and outer ventrolateral tubercles and are noticeably concave between the opposing outer ventrolaterals. An occasional rib may arise at the umbilical shoulder on one side but terminate on the opposite flank before reaching this point. Ribs may spring in pairs from the umbilical tubercles. The minor ribs carry siphonal, inner and outer ventrolateral tubercles. At the adoral end of the specimen the siphonal and outer ventrolateral tubercles are very subdued but the umbilicals and inner ventrolaterals are still marked. Impressions upon the dorsum indicate that in the preceding whorl the outer ventrolateral and siphonal tubercles were more strongly developed.

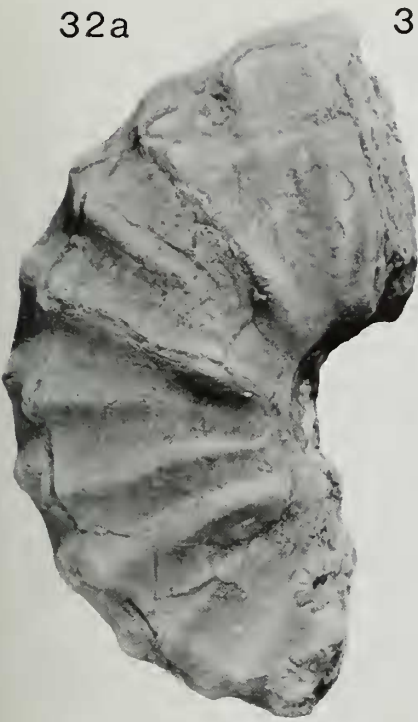
REMARKS. In its rather inflated whorls and relatively low rib density this specimen seems to be most closely comparable with *Pseudocalycoceras haughi* (Pervinqui re 1907: 270; pl. 14,

Fig. 32a, b *Acompsoceras calabarensis* sp. nov. Odukpani Formation (Lower Cenomanian), Calabar–Akamkpa road, 1.5 km north of junction with Calabar–Ikot Ekpene road. **Holotype** C.85250, $\times 1$. See also Fig. 30.

Fig. 33a, b *Acompsoceras* aff. *renevieri* (Sharpe). Odukpani Formation (Lower Cenomanian), Calabar–Akamkpa road, 1 km north of junction with Calabar–Ikot Ekpene road. C.85248, $\times 1$.

Fig. 34a, b *Pseudocalycoceras* cf. *haughi* (Pervinqui re). Odukpani Formation (Upper Cenomanian), from an uncertain locality, Calabar–Ikot Ekpene road. C.82111, $\times 1$.

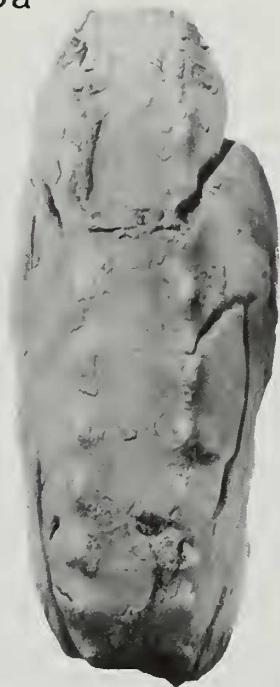
32a



32b



33a



33b



34a



34b



figs 1a, 1b). Kennedy *et al.* (1981: 48), in the most recent review of this genus, gave a list of possible synonyms of *P. haughi*. Of these, *P. paralouitense* (Basse 1940: 449; pl. 7, fig. 4; pl. 8, figs 2, 3; pl. 9, fig. 3) shows a very similar style and strength of ribbing, with the ribs bent back strongly over the venter just as in the Nigerian specimen. Although generally with narrower whorls, some examples of *P. paralouitense* may approach the breadth of the present specimen (see Basse 1940: pl. 9, fig. 3).

P. angolaense (Spath) (see Cooper 1978: 96) and the similar *P. dentonense* (Moreman) (see Cobban & Scott 1972) both show less inflated whorls with broader denser ribbing. *P. harpax* (Stoliczka 1865: 72; pl. 39, fig. 1) and *P. morpheus* (Stoliczka 1865: pl. 38, fig. 1) both have an ovoid compressed whorl section with the inner and outer ventrolateral tubercles closer together. The former is, in addition, much more densely ribbed.

Genus *CALYOCERAS* Hyatt, 1900

Subgenus *NEWBOLDICERAS* Thömel, 1972

TYPE SPECIES. *Acanthoceras newboldi* Kossmat, 1897; by the original designation of Thömel, 1972.

Calycomeras (Newboldiceras) annulatum Collignon, 1964

Figs 35, 36

1964 *Calycomeras annulatum* Collignon: 127; pl. 366, figs 1597, 1598.

? 1972 *Calycomeras (Calycomeras)* sp. aff. *annulatum* Collignon; Thömel: 64; pl. 16, figs 6, 7; pl. 18, figs 1, 2.

? 1973 *Calycomeras annulatum* Collignon; Cooper: 54, figs 8A–C.

? 1978a *Calycomeras (Conlinoceras) annulatum* Collignon; Cooper: 6.

MATERIAL AND OCCURRENCE. A single specimen (C.83477) from the Odukpani Formation (Middle Cenomanian), 30.3 km from Calabar.

DIMENSIONS.	D	Wb	Wh	U
C.83477	166	54 (32.5)	54 (32.5)	70 (42)
	116	48 (41)	42 (36)	–

DESCRIPTION. This specimen, reaching a diameter of 166 mm, consists of an adult(?) body chamber. It is evolute, the whorls being a little broader than high adapically but with whorl breadth equal to whorl height adorally. Intercostally the whorls are broadly rounded. The costal section is pentagonal at the adapical end of the specimen while adorally it is more nearly rounded (Fig. 35). There are 17 narrow ribs in this approximate half whorl. Each

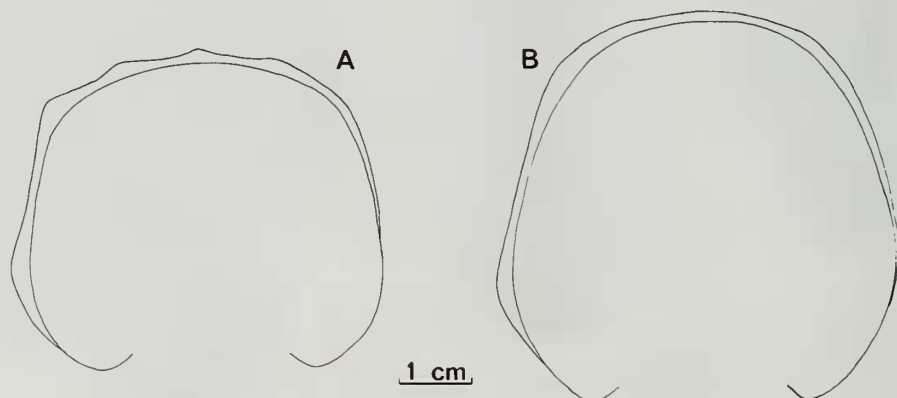


Fig. 35 Whorl sections in *Calycomeras (Newboldiceras) annulatum* Collignon. A, C.83477 at diameter of 115 mm; B, C.83477 at diameter of 160 mm.

originates on one side at a pronounced umbilical tubercle and bears on this side a fairly prominent inner ventrolateral tubercle. There are also subdued but definite outer ventrolateral tubercles and a siphonal tubercle at the adapical end of the specimen. On the opposite side, each rib lacks, or displays only a subdued, inner ventrolateral tubercle and dies out on the ventral part of the flank. Thus the ornament is markedly asymmetrical. Adorally the tubercles fade and at the largest preserved diameter only the umbilical tubercles are developed to any appreciable degree. At the adapical end of the specimen the ribs are rursiradiate and concave over the venter but adorally they are more nearly rectiradiate.

REMARKS. This specimen compares well with the Malagasy species *Calycoceras annulatum* Collignon (1964: 127; pl. 366, figs 1597, 1598), particularly in its wide umbilicus and narrow, distant ribs. Collignon reported the species from his 'Lower Cenomanian' (Zone of *Mantelliceras mantelli* and *Calycoceras newboldi*), but this zone seems to include younger Cenomanian for *C. newboldi* is characteristic of the Middle and Upper Cenomanian in north-west Europe (Kennedy & Hancock 1978: 15–16). *C. annulatum* has been referred to various of the subgenera proposed for *Calycoceras* by Thomel (1972) and Cobban & Scott (1972) (see reviews in Juignet & Kennedy 1976, Wright & Kennedy 1981). Thomel (1972: 64) included it in *C. (Calycoceras)* and Cooper (1978a: 6) in *C. (Conlinoceras)*. Its closest affinities, however, seem to lie with *C. (Newboldiceras)* (type species *Acanthoceras newboldi* Kossmat 1897: 4; pl. 1, figs 2a, 2b, 3a–c; pl. 3, fig. 2) with which it agrees in its large size and persistent polygonal whorl section and tubercles. It differs from the type species in its wider umbilicus and more distant ribs, but an intermediate form has been described by Pervinqui re (1907: 264; pl. 13, figs 1a, 1b).

Subfamily ACANTHOCERATINAE Grossouvre, 1894

Genus ACANTHOCERAS Neumayr, 1875

TYPE SPECIES. *Ammonites rhotomagense* Brongniart, 1822; by the subsequent designation of Grossouvre, 1894.

Acanthoceras robustum Crick, 1907

Fig. 37a, b

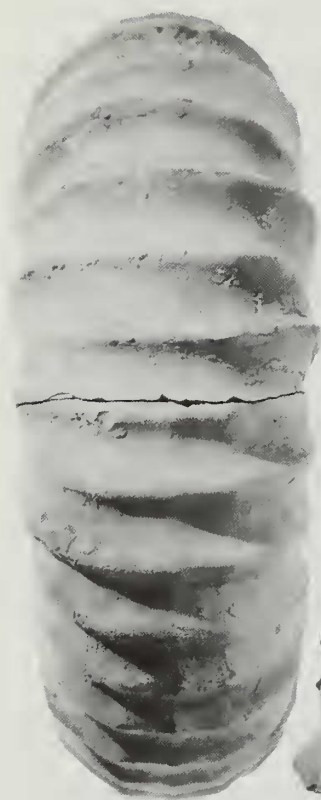
1907 *Acanthoceras robustum* Crick: 189.

1978 *Acanthoceras* sp. Kennedy: pl. 3, figs 6A, 6B.

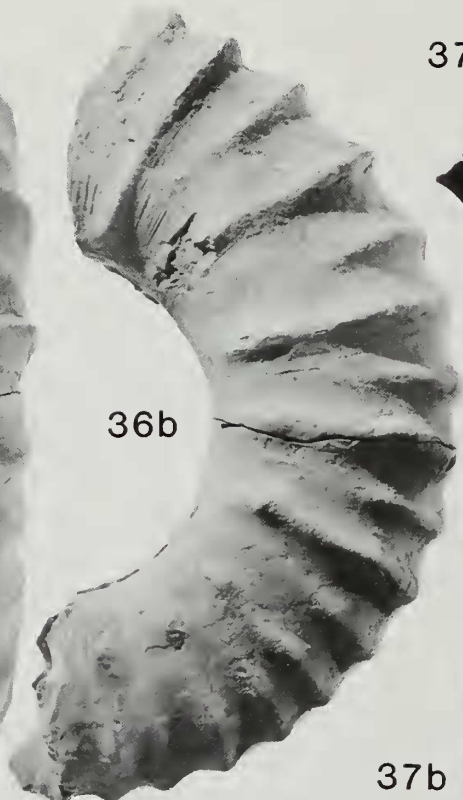
MATERIAL AND OCCURENCE. A single specimen (C.83551) from the Odukpani Formation (Middle Cenomanian), 32.2 km from Calabar.

REMARKS. This fragment belongs in the group of *Acanthoceras rhotomagense* (Brongniart). It finds its closest counterparts, however, not within the basal Middle Cenomanian (*Turrilites costatus* Zone) type population of Rouen, north-west France (see Kennedy & Hancock 1970), but in the population from Zululand described by Crick (1907). Crick (1907) proposed a number of species names (*Acanthoceras flexuosum*, *A. crassioratum*, *A. munitum*, *A. expansum*, *A. robustum*, *A. quadratum*, *A. hippocastanum* (non Sowerby) and *A. latum*) for members of this contemporaneous assemblage which differ only slightly from one another. As Kennedy (1971: 115–116; 1978: 22) has remarked, these forms probably represent variants of a single species. The present material agrees exactly in gross morphology and ornamentation with the variant given the name *A. robustum* by Crick (1907: 189). One (C.18189) of the three specimens (C.18188, C.18189 and C.18190, specimens 'a', 'b' and 'c' respectively in Crick 1907: 190) on which this species is based was figured by Kennedy (1978: pl. 3, figs 6A, 6B). When the Zululand fauna is revised *A. robustum* is likely to fall into synonymy.

The stratigraphic relationship between the Rouen and Zululand *Acanthoceras* populations is something of a problem. Although there is some morphological overlap (see Kennedy &



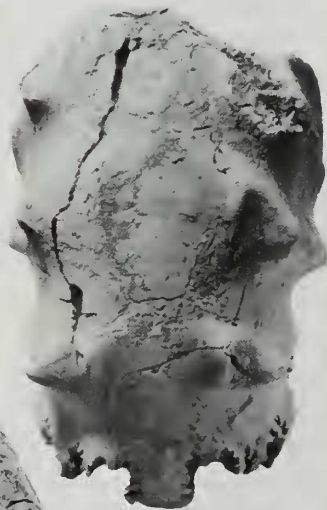
36a



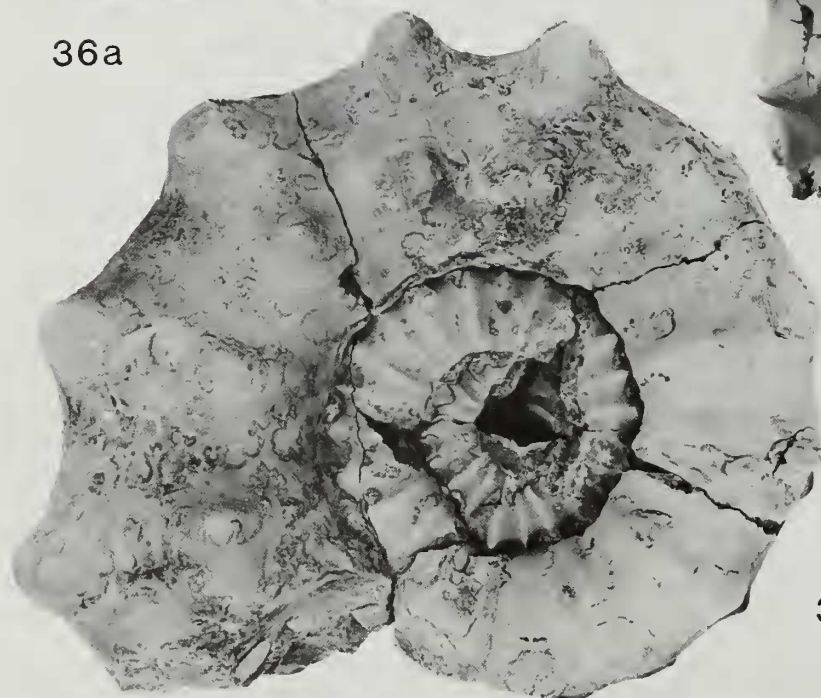
36b



37a



37b



38

Hancock 1970: 487), overall population structure is different. Partly on the basis of the associated *Calycoceras*, Kennedy (1971: 115–116) thought the Zululand fauna to be somewhat younger than that at Rouen, placing it above the *Turrilites acutus* assemblage as typically developed in southern England but below the overlying *Acanthoceras jukesbrownei* assemblage. In Zululand, however, the *Calycoceras* fauna occurs slightly above the one with *Acanthoceras* (Kennedy & Klinger 1975: 277; Kennedy 1978: 5), and Juignet & Kennedy (1976: 119) were undecided whether the differences between the Rouen and Zululand populations were the result of stratigraphical or geographical variation. In southern England the Zululand 'species' *A. latum* Crick occurs in the *T. acutus* Zone (Kennedy 1971: 89), occurring at a higher level than the Rouen fossil bed. The Nigerian specimen too occurs above beds exposed 27.9 km from Calabar which seem to correspond with the *T. costatus* Zone (see p. 59).

Acanthoceras amphibolum Morrow, 1935

Figs 38–41

- 1935 *Acanthoceras?* *amphibolum* Morrow: 470; pl. 49, figs 1–4, 6; pl. 51, figs 3, 4.
 1952 *Acanthoceras hazzardi* Stephenson: 201; pl. 48, figs 1, 2; pl. 49, fig. 4.
 1963 *Paracanthoceras amphibolum* (Morrow) Haas: 18.
 1965 *Plesiakanthoceras amphibolum* (Morrow) Hattin: pl. 4, figs J, K; pl. 5, figs C–F.
 1966 *Acanthoceras amphibolum* Morrow; Matsumoto & Obata: 45; text-figs 4–6.
 1968 *Acanthoceras amphibolum* Morrow; Hattin: 1087.
 1969 *Acanthoceras amphibolum* Morrow; Matsumoto, Muramoto & Takahashi: 266; pl. 31, figs 1a, 1b.
 1972 *Acanthoceras amphibolum* Morrow; Cobban & Scott: 65; pl. 9; pl. 10, figs 12–16.
 1977 *Acanthoceras amphibolum* Morrow; Cobban: 23; pl. 8, figs 8, 9; pl. 12, figs 10–12, 15–23.
 1978 *Acanthoceras amphibolum* Morrow; Kauffman *et al.*: pl. 4, figs 1, 2.

MATERIAL AND OCCURRENCE. Nine specimens (C.83115, C.83117–8, C.83472–4, UIN 473.1–3) from the Odukpani Formation (Middle Cenomanian), 30.1 km from Calabar.

DIMENSIONS.	D	Wb	Wh	U
C.83472	215	72 (33.5)	70 (32.5)	90 (42)
C.83473	170	65 (38)	60 (35)	70 (41)
C.83118	135	56 (41.5)	51 (37.8)	56 (41.5)

DESCRIPTION. The shell is evolute and reaches a diameter in excess of 200 mm. The whorls are only a little broader than high, the flanks and the venter being flattened in early ontogeny but towards adulthood the flanks become slightly convex.

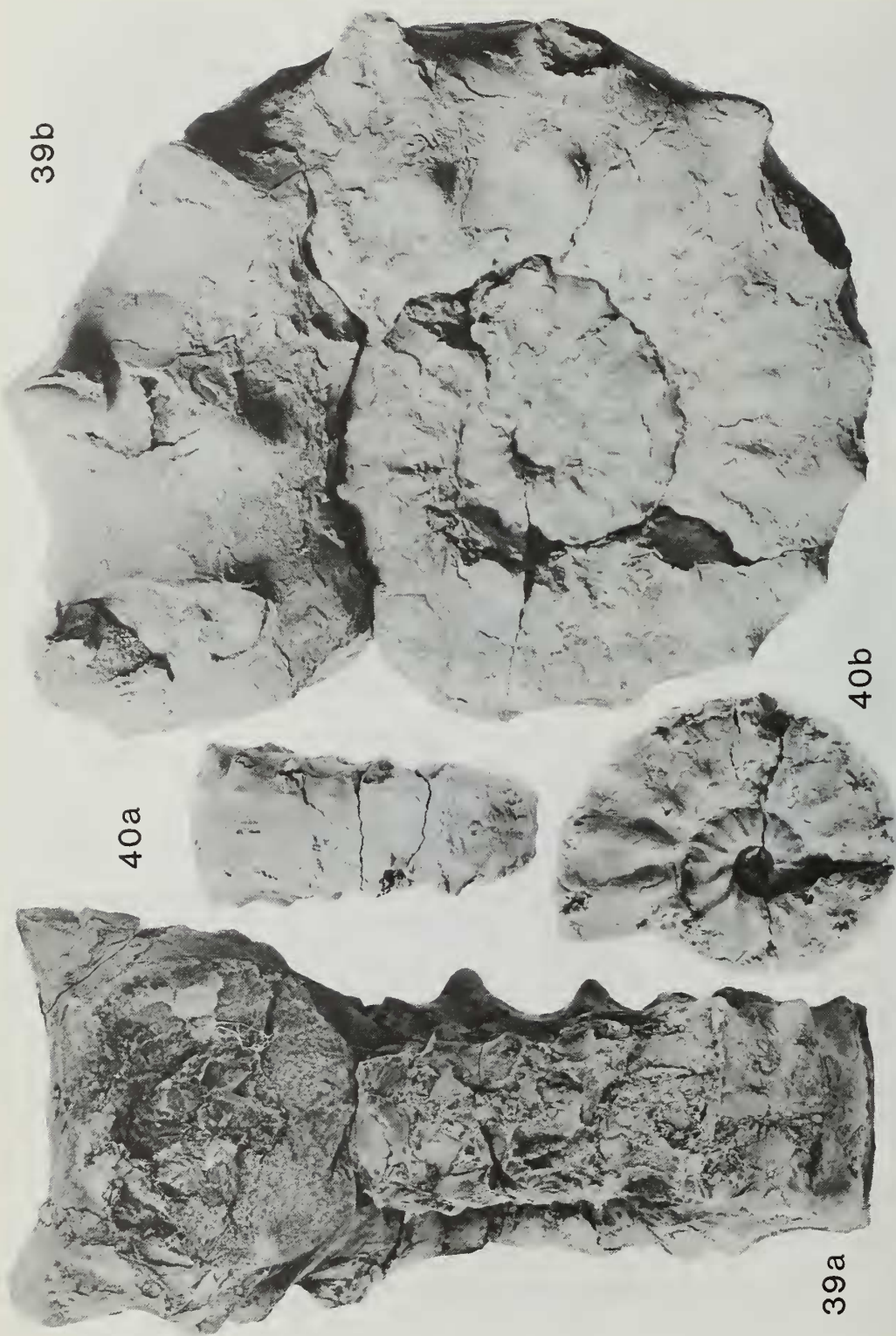
The earliest whorls are smooth and unstricted. At a diameter of about 6 mm ribs, which carry rather prominent inner ventrolateral tubercles, appear on the flanks. The umbilical tubercles, which are inconsistently developed, are sometimes strong and bullate, sometimes highly effaced and often absent altogether. There are also outer ventrolateral and siphonal tubercles.

Between diameters of 26 and 70 mm the number of major ribs increases from about 14 or 15 to about 18 in each whorl. Each originates from a bullate, pointed umbilical tubercle, again often effaced to a greater or lesser degree. There is a pair of prominent inner ventrolateral tubercles, a pair of variably-developed outer ventrolaterals and a low clavate siphonal tubercle. The outer ventrolaterals are normally markedly clavate and often asymmetrical, with the steeper face at the adoral end, but sometimes they are conical or

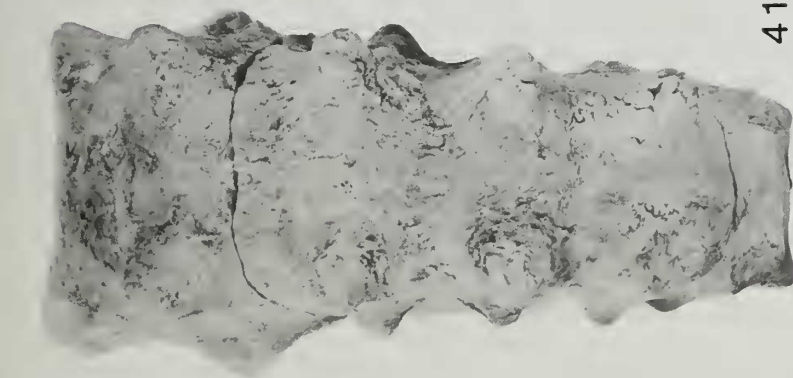
Fig. 36a, b *Calycoceras* (*Newboldiceras*) *annulatum* Collignon. Odukpani Formation (Middle Cenomanian), 30.3 km from Calabar. C.83477, $\times 0.65$. See also Fig. 35.

Fig. 37a, b *Acanthoceras robustum* Crick. Odukpani Formation (Middle Cenomanian), 32.2 km from Calabar. C.83551, $\times 0.75$.

Fig. 38 *Acanthoceras amphibolum* Morrow. Odukpani Formation (Middle Cenomanian), 30.1 km from Calabar. C.83473, $\times 0.65$. See also Figs 39–41.



Figs 39, 40 *Acanthoceras amphibolum* Morrow. Odukpiani Formation (Middle Cenomanian), 30.1 km from Calabar. Fig. 39a, b, C.83472, $\times 0.65$. Fig. 40a, b, C.83474, $\times 1$. See also Figs 38, 41.



41



42a



42b

Fig. 41 *Acanthoceras amphibolum* Morrow. Odukpani Formation (Middle Cenomanian), 30.1 km from Calabar. C.83473, $\times 0.65$, ventral view of specimen shown in Fig. 38. See also Figs 39, 40.

Fig. 42a, b *Acanthoceras* sp. Odukpani Formation (Middle Cenomanian), 30.1 km from Calabar. C.83116, $\times 0.75$.

situated a little adoral of the inner ventrolaterals and connected to them by obliquely directed swellings. Intercalated at irregular intervals there are minor ribs bearing a siphonal tubercle and a pair of outer ventrolateral tubercles, and sometimes in addition a pair of inner ventrolaterals; they may extend some distance across the flank and approach the development of those major ribs carrying effaced umbilical tubercles.

At diameters in excess of 90 mm the outer ventrolateral and siphonal tubercles tend to fade, although low extended siphonal swellings may persist up to a diameter of some 120 mm forming an inconspicuous keel; broad low outer ventrolateral swellings may still occur at diameters of 100 mm or more. The number of ribs decreases at this stage: there are 12 to 16 ribs on the whorl between diameters of 80 and 170 mm. The inner ventrolateral and umbilical tubercles enlarge greatly at this stage. The umbilical tubercles are conical to bullate in shape and are consistently well developed. The ventrolaterals are rounded and conical at first, but later may become dorsoventrally expanded into wing-like structures. The umbilical and inner ventrolateral tubercles are joined by broad rounded ribs. There may be a siphonal depression between the opposing inner ventrolaterals or a flattened area may develop here. Occasionally, broad, vague, rib-like structures may be intercalated with the main ribs over the venter. The whorl sides are convexly rounded at this stage, the greatest breadth being just dorsal of the umbilical tubercle. As maximum size is approached the ribs become even more distant and the umbilical tubercles migrate towards the mid-flank region.

REMARKS. This material is readily comparable with *Acanthoceras amphibolum* Morrow, a common species in Texas (Stephenson 1952, Young & Powell 1978) and the western interior of the United States (Cobban & Scott 1972, Cobban 1977), which also occurs in Japan (Matsumoto *et al.* 1969) and probably in southern England (Matsumoto *et al.* 1969: 268). This species (see Morrow 1935, Hattin 1965, Cobban & Scott 1972, Cobban 1977) has a very similar ontogenetic development. In its early stages there is occasional multiplication of the siphonal tubercles and the outer ventrolaterals may be asymmetrically clavate. The siphonal tubercles fade, although a low keel may persist, and at adulthood there are massive inner ventrolateral and umbilical tubercles just as in the present specimens.

A series of hypernodose acanthoceratids occurs in the Middle Cenomanian of the western interior of the U.S.A. Of these, *Acanthoceras alvaradoense* Moreman (1942: 205; pl. 32, fig. 6; Stephenson 1955: 63; pl. 7, figs 1–9; Cobban 1977: 24; pl. 6, figs 1–7, 11–20) is very similar to *A. amphibolum* in its general ontogenetic development and adult morphology. According to Cobban (1977: 24), *A. alvaradoense* differs only in its earliest whorls, which bear constrictions at diameters of 10–12 mm, and in its less clavate outer ventrolateral and siphonal tubercles. There is no sign of constrictions in the Nigerian specimens and their siphonal and outer ventrolateral tubercles are normally markedly clavate. Another of these western interior forms is '*Plesiacanthoceras*' *wyomingense* (Reagan) (see Haas 1963, 1964). Again its adult morphology is close to that of the present material, although its umbilical tubercles do not appear to be so consistently well developed and its ventrolaterals may be highly spinose at this stage. In addition the outer ventrolateral tubercles appear to be even more clavate in the juvenile stages, while in the middle whorls there are twice as many ventrolateral as umbilical tubercles.

A Moroccan specimen described by Collignon (1966: 28; pl. 14; pl. 15, figs 1, 1a) as '*Euomphaloceras cornutum* (Kossmat)' does not seem to be conspecific with Kossmat's (1895: 11; pl. 5, figs 1a–c) *Acanthoceras cunningtoni* var. *cornuata* (itself a synonym of *Euomphaloceras cunningtoni cunningtoni* (Sharpe)). Instead its adult whorls resemble those in the present material but the details of its early stages are unknown.

Acanthoceras sp.
Fig. 42a, b

MATERIAL AND OCCURRENCE. A single specimen (C.83116) from the Odukpani Formation (Middle Cenomanian), 30.1 km from Calabar.

DIMENSIONS.	D	Wb	Wh	U
C.83116	155	—	—	65 (42)
	86	34 (39.5)	32 (37)	33 (38)
	58	24 (41)	23 (39.6)	20 (34.5)

DESCRIPTION. This fully septate specimen has a diameter of 155 mm, and is evolute with more or less quadrate whorls.

In the earliest stages seen (between diameters of 15 and 20 mm) there are pointed inner ventrolateral tubercles each joined by an obliquely-directed swelling to a conical or clavate outer ventrolateral tubercle which is situated a little further adorally. There are low clavate siphonal tubercles tending to form an intermittent keel. There appear to be rather poorly developed umbilical tubercles at this stage corresponding to only some of the inner ventrolaterals. Low rounded ribs extend from the inner ventrolateral tubercles for a greater or lesser distance across the flanks. The umbilical tubercles are situated on the more persistent of these ribs. There are about nine rows of inner ventrolateral tubercles in each half whorl at this stage.

By a diameter of about 40 mm the umbilical tubercles are more prominent, as are the flank ribs. There are more inner ventrolateral than umbilical tubercles.

At diameters between about 55 and 85 mm there are 10 or 11 ribs per half whorl. They are narrow, high, rounded and unevenly spaced. Most bear a prominent, bullate, pointed umbilical tubercle but its strength varies and on every second to fifth rib it is markedly effaced. Each rib also bears a pair of inner ventrolateral tubercles, which are usually prominent and pointed but occasionally also weakly developed, joined by oblique swellings to corresponding conical or slightly clavate outer ventrolaterals. At this stage there are only faint, rounded, conical or clavate siphonal tubercles which are irregularly spaced and not always located exactly between the outer ventrolaterals. Occasional intercalated ventral ribs each bearing a low siphonal tubercle and a pair of weak outer ventrolaterals occur. They carry no inner ventrolateral tubercles but may pass onto the ventral part of the flank.

The remainder of the specimen is poorly preserved. In its last half whorl there are 12 narrow, rounded inequidistant ribs. The strength of the umbilical tubercles varies markedly. They may be so effaced as to be practically non-existent, but some are pronounced bullate structures: all intermediate strengths occur in no regular or consistent manner. The venter is unclear, but appears to be flattened. There is a ventrolateral horn on each rib but it seems to be only a low rounded cone.

The suture is rather finely subdivided with a deep E and a rather complex L.

REMARKS. In its early whorls this specimen is difficult to distinguish from the contemporary material of *Acanthoceras amphibolum* described above, agreeing in the occasional multiplication of the siphonal and outer ventrolateral tubercles and in the variable development of the umbilical tubercles. In the present individual, however, the latter character is exaggerated and persists into the adult stages, where the ribbing is denser and the ventrolateral tubercles weaker. This specimen does not conform closely to any other known species and probably represents a variant of *A. amphibolum*: the similarity of the two forms in their earlier stages seems to indicate a close relationship. Due to the paucity of the material at hand, however, the precise nature of this relationship and the appropriate taxonomic rank for this specimen are difficult to decide.

Subfamily EUOMPHALOCERATINAE Cooper, 1978

Genus EUOMPHALOCERAS Spath, 1923a

TYPE SPECIES. *Ammonites euomphalus* Sharpe, 1855; by the original designation of Spath, 1923a.

Euomphaloceras inerme (Pervinqui re, 1907)

Fig. 44a, b

- 1826 *Ammonites rhotomagensis* J. de C. Sowerby: 25; pl. 515 (lower figure only).
 1855 *Ammonites sussexiensis* Mantell; Sharpe: 34; pl. 15, figs 1a–d.
 1907 *Acanthoceras cunningtoni* var. *inermis* Pervinqui re: 277.
 1923a *Acanthoceras sussexiense* (Mantell); Spath: 144.
 1926 *Acanthoceras evolutum* Spath: 82.
 1951 *Acanthoceras evolutum* Spath; Wright & Wright: 28.
 1957 *Acanthoceras* aff. *evolutum* Spath; Matsumoto, Saito & Fukada: 33; pl. 14, fig. 2.
 1971 *Euomphaloceras inerme* (Pervinqui re) Kennedy: 94; pl. 59, figs 6a, 6b; pl. 61, figs 1a, 1b; pl. 62, figs 1a, 1b; pl. 64, fig. 1.

MATERIAL AND OCCURRENCE. Eleven specimens (C.82110, C.82141, C.82143, C.82147, C.83091, C.85264, UIN 477.1–5) from the Odukp ni Formation (Middle Cenomanian), 27.9 km from Calabar.

DESCRIPTION. The shell is evolute, reaching a diameter of some 300 mm. The whorl breadth is equal to, or a little greater than, the whorl height. The greatest intercostal breadth is at the level of the umbilical tubercles.

The earliest whorls are not seen. In the whorl up to a diameter of 70 mm there are about 18 major ribs. Each rib originates at a bullate umbilical tubercle and carries a pair of moderately spinose inner ventrolateral tubercles and pronounced clavate, rounded or pyramidal outer ventrolateral tubercles, and a more subdued, rounded or clavate siphonal tubercle. Alternating with the major ribs over the venter are one or more minor ribs which do not extend onto the whorl sides. The minor ribs carry a pair of outer ventrolateral tubercles, which are generally less pronounced than those of the major ribs and sometimes absent altogether, and a single siphonal tubercle of more or less equal strength to those of the major ribs.

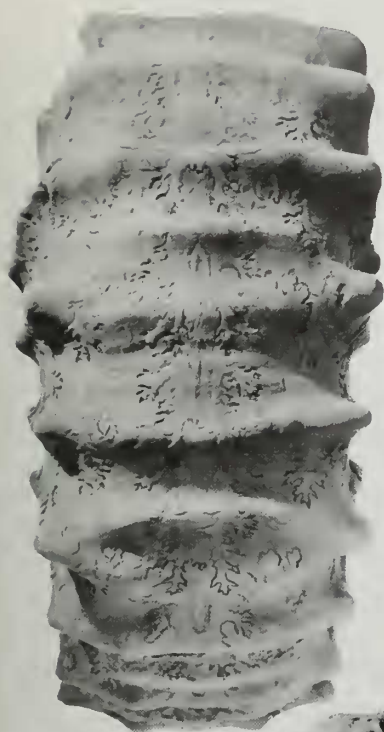
At diameters in excess of 70 mm the minor ribs tend to disappear, but persist in some individuals up to a diameter of over 100 mm. At these large diameters the minor ribs, when present, may be markedly convex. The major ribs increase in number to 20 or more in each whorl and are narrow, rounded and may be concave on the flanks. The umbilical, inner and outer ventrolateral tubercles appear only as swellings on the ribs. Along the siphonal line there may be a low swelling or a depression. At adulthood the inner and outer ventrolateral tubercles are difficult to distinguish as discrete swellings. The siphonal swellings tend to disappear, the ribs being uninterrupted over the venter or with a siphonal depression. The number of ribs decreases to 15 or 16 in each whorl at this stage.

The suture has a deep E, a highly subdivided bifid E/L and a highly subdivided L.

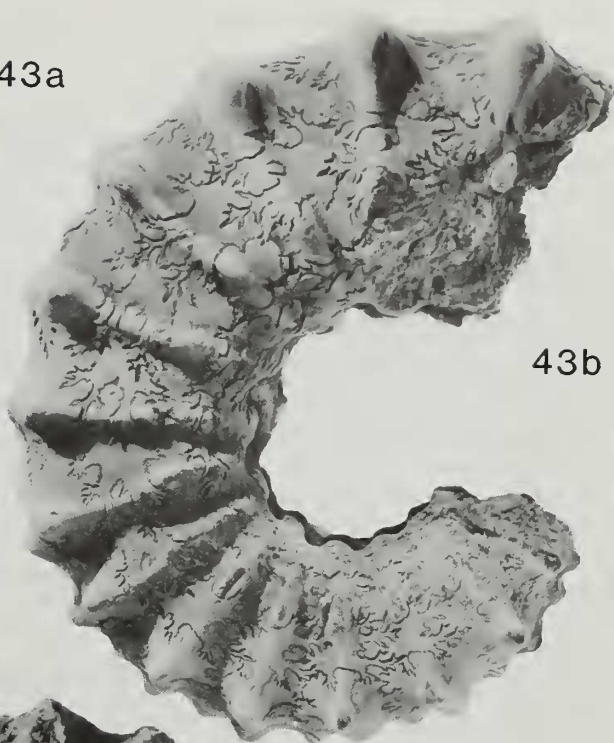
REMARKS. This material is most closely comparable with *Euomphaloceras inerme* (Pervinqui re). The English material of this species, including the holotype, was described by Kennedy (1971: 94) and agrees in ontogenetic development and ornamentation with the Nigerian specimens. The development of the minor ribbing is variable in the Nigerian material, however, and densely ribbed variants may show a ventral ornament like that in *E. cunningtoni* (see pp. 42–51) although this species has markedly fewer major ribs. In other specimens the intercalated ribs are lost early in ontogeny, these individual coming to resemble the low Middle Cenomanian *Acanthoceras rhotomagense* var. *sussexiense* (Mantell 1822: 114; pl. 20, fig. 2; Kennedy & Hancock 1970: 472; pl. 89, fig. 2; pl. 91, figs 1, 2; pl. 92, figs 1, 2; text-figs 3, 4, 5, 6a). Specimens of this form transitional to *Euomphaloceras* also occur at Rouen, France (Kennedy & Hancock 1970: 474; pl. 92, fig. 4; pl. 93).

Fig. 43a, b *Euomphaloceras cunningtoni meridionale* (Stoliczka). Odukp ni Formation (Middle Cenomanian), 27.9 km from Calabar. C.82104, $\times 0.65$. See also Figs 45, 46.

Fig. 44a, b *Euomphaloceras inerme* (Pervinqui re). Odukp ni Formation (Middle Cenomanian), 27.9 km from Calabar. C.85264, $\times 0.75$.



43a



43b



44a



44b

Euomphaloceras cunningtoni (Sharpe, 1855)

- 1855 *Ammonites cunningtoni* Sharpe: 35; pl. 15, figs 2a-c.
 1863 *Ammonites cunningtoni* Sharpe; Pictet: 51; pl. 5, figs 2a-c (only).
 1864 *Ammonites meridionalis* Stoliczka: 76; pl. 41, figs 1a-c.
 1897 *Acanthoceras cunningtoni* var. *cornuata* Kossmat: 11; pl. 5, figs 1a-c.
 ? non 1904 *Acanthoceras cunningtoni* (Sharpe); Douvillé: 241; pl. 31, fig. 2.
 1907 *Acanthoceras cunningtoni* (Sharpe); Pervinquière: 277; pl. 15, figs 1a-c.
 1907 *Acanthoceras meridionale* (Stoliczka) Pervinquière: 278; pl. 15, figs 2-6.
 1928 *Acanthoceras lonsdalei* Adkins: 244; pl. 26, fig. 5; pl. 27, fig. 3.
 1933 *Acanthoceras cunningtoni* (Sharpe); Collignon: 63, figs 2, 3.
 non 1940 *Acanthoceras meridionale* (Stoliczka) var. *multicostata* Basse: 446; pl. 6, figs 2a, 2b.
 ? 1940 *Cunningtoniceras cunningtoni* (Sharpe) Fabre: 234; pl. 8, fig. 5.
 1944 *Cunningtoniceras höltkeri* Erni: 470; pl. 11.
 1951 *Euomphaloceras euomphalum* (Sharpe); Wright & Wright: 29 (*pars*).
 1952 *Acanthoceras? eulessanum* Stephenson: 201; pl. 47, fig. 5; pl. 48, figs 3, 4.
 1955 *Euomphaloceras lonsdalei* (Adkins) Stephenson: 62; pl. 6, figs 6-20.
 1957 *Euomphaloceras* cf. *euomphalum* (Sharpe); Matsumoto, Saito & Fukada: 34; pl. 15, fig. 3.
 1963 *Euomphaloceras cunningtoni* (Sharpe) Wright: 607; pl. 88, fig. 2; pl. 89, fig. 1.
 1963 *Euomphaloceras lonsdalei* (Adkins); Wright: 609; pl. 87, fig. 2; pl. 88, fig. 1; pl. 89, fig. 2.
 1964 *Euomphaloceras euomphalum* var. *pervinquieri* Collignon: 145; pl. 373, fig. 1619.
 ? non 1966 *Euomphaloceras cornutum* (Kossmat); Collignon: 28; pl. 14; pl. 15, figs 1, 1a (?= *Acanthoceras amphibolum* Morrow).
 1966 *Euomphaloceras pervinquieri* Collignon: 29.
 1969 *Euomphaloceras meridionale* (Stoliczka); Matsumoto, Muramoto & Takahashi: 272; pl. 33, figs 1, 2; pl. 34, fig. 1; text-fig. 6.
 1971 *Euomphaloceras cunningtoni* (Sharpe); Kennedy: 92; pl. 60, figs 1a, 1b; pl. 61, figs 2a, 2b.
 1972 *Euomphaloceras* cf. *E. cunningtoni* (Sharpe); Cobban & Scott: 70; pl. 4, figs 4, 5; pl. 5, figs 6-8.
 1972 *Euomphaloceras cunningtoni* (Sharpe); Thomel: 163; pl. 71, fig. 4; pl. 83; pl. 85, fig. 2; pl. 86, figs 1, 2; pl. 87, figs 1-6.
 1972 *Euomphaloceras meridionale* (Stoliczka); Thomel: 165.
 1973 *Euomphaloceras cunningtoni meridionale* (Stoliczka); Cooper: 61, figs 10A, 10B, 11, 12A, 12B, 13A.
 ? 1977 *Euomphaloceras* aff. *E. cunningtoni* (Sharpe); Cobban: 25; pl. 11, figs 17, 18.
 1978 *Euomphaloceras cunningtoni* (Sharpe); Wiedmann & Kauffman: pl. 5, fig. 5.
 1978 *Euomphaloceras lonsdalei* (Adkins); Young & Powell: pl. 5, figs 1, 7.
 1978a *Euomphaloceras cunningtoni meridionale* (Stoliczka); Cooper: 6, fig. 8.

REMARKS. Members of the *Euomphaloceras cunningtoni* group are significant elements of Middle Cenomanian faunas. They have a virtually global distribution occurring in Europe, the Middle East, north and west Africa, the Malagasy Republic, India, Australasia, Japan and the United States. Their ornamentation varies widely and this, coupled with the lack of large population samples, has led to much debate concerning their precise relationships and distinguishing characters. The two main representatives, *E. cunningtoni* (Sharpe) and *E. meridionale* (Stoliczka), were considered by Matsumoto *et al.* (1969) and Thomel (1972) to be distinct species. Matsumoto *et al.* (1969: 275) distinguished *E. meridionale* on the basis of its more obvious multiplication of the ribs over the venter, each rib bearing a siphonal and a pair of outer ventrolateral tubercles; the bifurcation of the ribs at the inner ventrolateral tubercles; the predominantly lateral extension of the last-mentioned tubercles; and by its broad whorls. Thomel (1972: 165) also stressed the multiplication of both the siphonal and the outer ventrolateral tubercles in *E. meridionale* but considered its adult morphology to be distinctive as well, there being prominent horns while *E. cunningtoni* displays ribs without prominent tubercles at large diameters. Wright (1963: 608) has also remarked upon the differences in ventral ornamentation, but considered them to warrant only subspecific

separation, a conclusion adopted by Kennedy (1971: 93). One of the main problems in this group is the relatively meagre amount of material. The recovery, from a single horizon in the Odukpani Formation, of the 99 specimens referred to *E. cunningtoni cunningtoni* (Sharpe), below, allows improved understanding of individual variation. These specimens show considerable inconsistency in their ornamental details and although the population is centred on a morphology close to *E. cunningtoni* many individuals are of a decidedly *E. meridionale* character. Another smaller collection, from a horizon some 30–35 m below the first, contains individuals of a more consistently *E. meridionale* type. The youngest material of this group in the Odukpani Formation represents a new form described here and assigned to *E. cunningtoni alatum* subsp. nov. These three forms seem to represent stratigraphically successive subspecies whose mean population structure is slightly different but which show considerable overlap between the end members. Such a situation was suspected by Kennedy & Hancock (1977: 135). Younger forms in the Odukpani Formation display a lesser tendency towards multiplication of the ventral ribbing and tuberculation, but in their adult stages show increasingly pronounced ventrolateral ornament.

In Texas and the western interior of the United States the *E. cunningtoni* group is most commonly represented by *E. lonsdalei* (Adkins 1928: 244; pl. 26, fig. 5; pl. 27, fig. 3; Stephenson 1955: 62; pl. 6, figs 6–20). *E. lonsdalei* is close to *E. cunningtoni cunningtoni* but differs in its less depressed whorl section, rather denser major ribbing and reduced multiplication of the ventral ribs and tubercles. Variation within the present Nigerian material indicates that *E. lonsdalei* does not deserve separation at the species level but is best regarded as another subspecies of *E. cunningtoni* (see also Kennedy 1971: 93–94). In Texas Stephenson (1955: 201) reported *E. cunningtoni lonsdalei* in beds a little above those containing *Acanthoceras euleusanum* Stephenson, a synonym of *E. cunningtoni cunningtoni*. A similar sequence occurs in Colorado (Cobban & Scott 1972: pl. 40). Here, forms close to *E. cunningtoni cunningtoni* occur in the lower part of the Middle Cenomanian, while *E. cunningtoni lonsdalei* characterizes higher beds in the Zone of *Acanthoceras muldoonense*.

It appears, therefore, that changes in ornamental details in this group are the result of age differences. Since individual variation may be important, however, accurate diagnosis of members of the group may require large population samples. For this reason no comprehensive attempt is made here to assign those previously described specimens to a particular subspecies. Reasonably secure determinations are, nevertheless, indicated below.

Euomphaloceras cunningtoni meridionale (Stoliczka, 1864)

Figs 43, 45, 46

1864 *Ammonites meridionalis* Stoliczka: 76; pl. 41, figs 1a–c.

MATERIAL AND OCCURRENCE. Eight specimens (C.82104, C.82139, C.82142, C.83092, UIN 478.1–4) from the Odukpani Formation (Middle Cenomanian), 27.9 km from Calabar.

DIMENSIONS.	D	Wb	Wh	U
C.83092	165	90 (54.5)	68 (41)	61 (37)

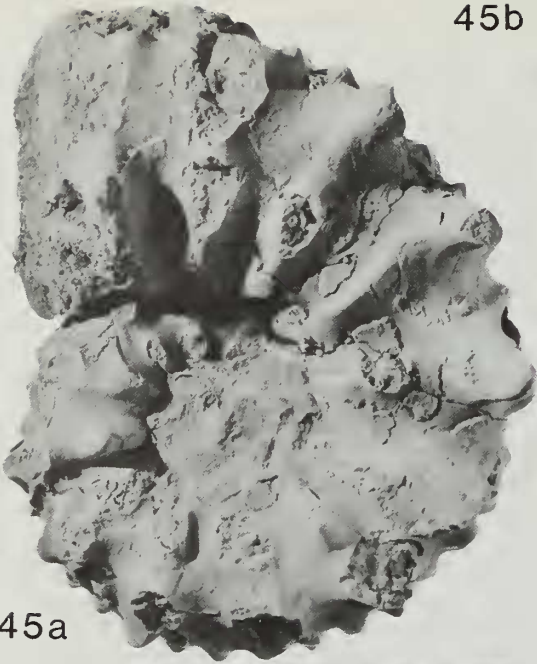
DESCRIPTION. The shell is evolute, reaching a diameter of over 230 mm. The whorls are broader than high, the greatest intercostal breadth being at the level of the umbilical tubercles.

In C.82139 there are 12 or 13 major ribs in the complete whorl between diameters of 35 and 90 mm; their frequency increases during ontogeny. In the middle growth stages in C.83092 there are 16 or 17 in each whorl. On the flank each major rib generally bears a prominent, bullate pointed umbilical tubercle, although this may occasionally be effaced, and a long, usually spinose inner ventrolateral tubercle extended chiefly in a lateral direction. Over the venter the major ribs normally bifurcate at the inner ventrolateral tubercles and a further minor rib is usually intercalated with these looped pairs of ribs. Over the venter each rib bears a pair of prominent rounded outer ventrolateral tubercles and a

45b



45a



46a



46b

Figs 45, 46 *Euomphaloceras cunningtoni meridionale* (Stoliczka). Odukpani Formation (Middle Cenomanian), 27.9 km from Calabar. Fig. 45a, b, C.82139, $\times 1$. Fig. 46a, b, C.83092, $\times 0.65$. See also Fig. 43.

more subdued siphonal tubercle which becomes decreasingly conspicuous as growth proceeds. The outer ventrolaterals immediately adjacent to the inner ventrolateral tubercles may be especially prominent. In one specimen (UIN 478.3) the outer ventrolateral tubercles are markedly clavate in places and each corresponds to two siphonal tubercles.

At diameters in excess of 150 mm neither the umbilical nor the inner ventrolateral tubercles develop into horns or spines. The ornament here consists of narrow, rounded ribs, often concave on the flanks, upon which the umbilical, inner and outer ventrolateral tubercles manifest themselves as bullate rounded swellings. In the siphonal region there may be a faint swelling or a depression on the ribs, or they may be broadly arched. An occasional rib runs obliquely across the venter, not meeting its fellow on the opposite side but terminating before reaching the ventrolateral shoulder. At these large diameters there are still some minor ribs alternating with the major ribs over the venter. They may be broadly arched structures or show swellings at the level of the outer ventrolateral tubercles and, less commonly, along the siphonal line. There appear to be more than 20 major ribs in each whorl at this stage.

The suture is fairly complex with E deep, E/L large, bifid and florid and L broad, deep and highly subdivided.

REMARKS. This population conforms closely with *Euomphaloceras cunningtoni meridionale* (Stoliczka 1864: 76; pl. 41, figs 1a-c) in gross morphology, ornament, suture pattern and in the persistence of minor intercalated ribs at large diameters. In the Nigerian material, tubercle development is suppressed during the later growth stages although Stoliczka (1864: 76) mentioned long, thick ventrolateral spines in his large specimens. A similar variation in adult ornamentation exists between material of *E. cunningtoni cunningtoni* described by Thomel (1972) and that dealt with below.

The differences between the material referred here to *E. cunningtoni meridionale* and that to *E. cunningtoni cunningtoni* are largely a matter of overall population structure. *E. cunningtoni meridionale* is characterized by the generally equal multiplication of its siphonal and outer ventrolateral tubercles, by the bifurcation of the major ribs over the venter, by its more persistent minor ribs and by not showing amalgamation of the inner and outer ventrolateral tubercles at large diameters.

Apart from the lectotype (see Stoliczka 1864: pl. 41, figs 1a-c), little of the previously described material can be confidently assigned to this subspecies, but specimens figured by Matsumoto *et al.* (1969: pl. 33, figs 1, 2; pl. 34, fig. 1) may well belong here.

Euomphaloceras cunningtoni cunningtoni (Sharpe, 1855)

Figs 47-52

1855 *Ammonites cunningtoni* Sharpe: 35; pl. 15, figs 2a-c.

MATERIAL AND OCCURRENCE. Ninety-nine specimens (C.83097-102, C.83431-66, UIN 422.1-57) from the Odukpani Formation (Middle Cenomanian), 28.3 km from Calabar.

DIMENSIONS.	D	Wb	Wh	U
C.83431	110	41 (37)	39 (35.5)	42 (38)
C.83097	100	37 (37)	36 (36)	40 (40)
C.83099	91	41 (45)	35 (38.5)	33 (36)
C.83100	85	28 (33)	31 (36.5)	32 (37.7)
C.83434	65	28 (42.4)	27 (41)	20 (30.7)

DESCRIPTION. The shell is evolute, the umbilicus widening during ontogeny. Whorl breadth may be distinctly greater than its height or the whorls may be higher than broad. The venter and the flanks are flattened in the early stages but tend to become rounded later on. The largest of the present specimens has a diameter of some 150 mm.

In the middle growth stages the ornamental details are highly variable. In each whorl there are about 12 major ribs which are rounded and narrower than the interspaces. On the flank,

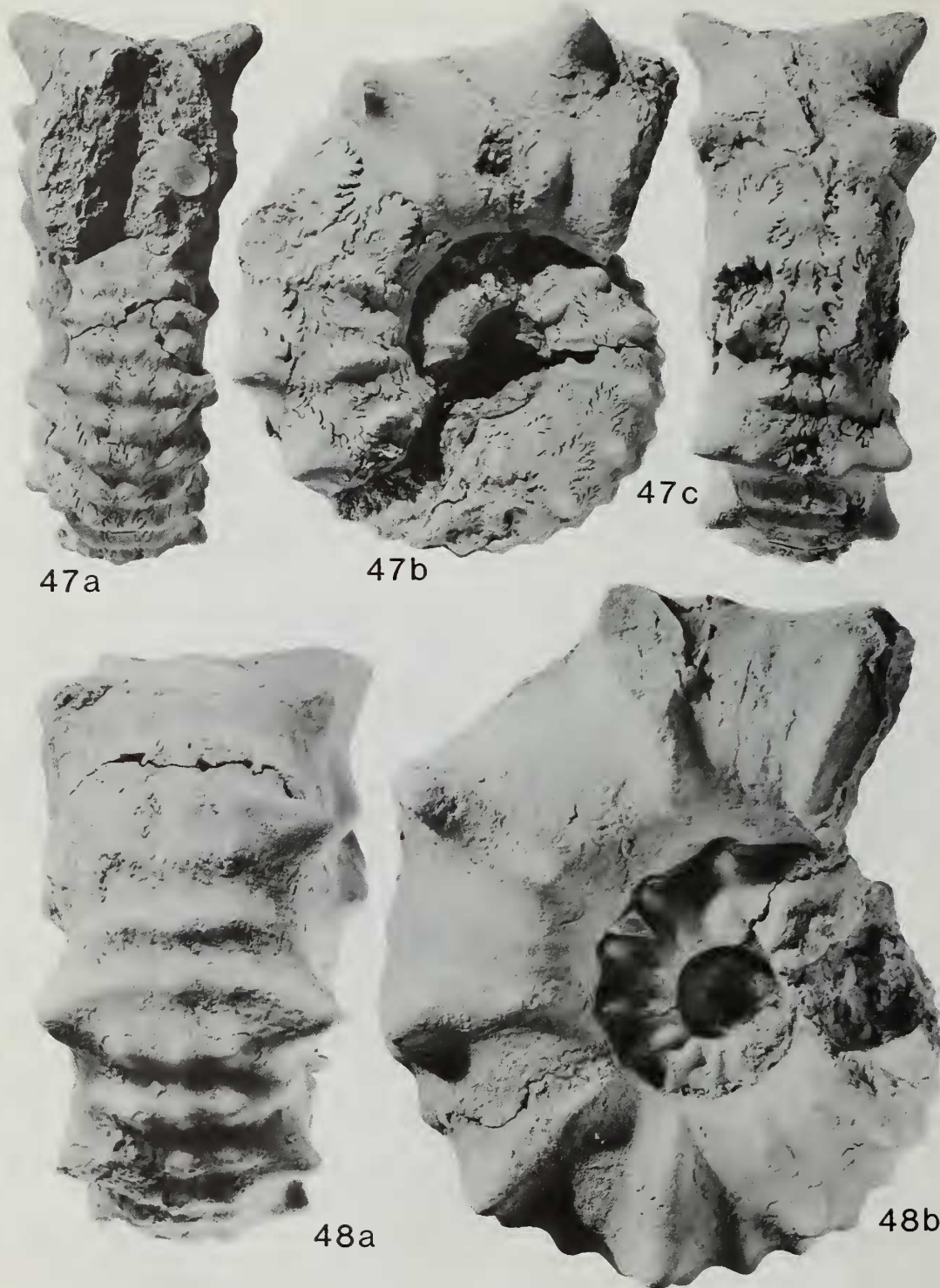
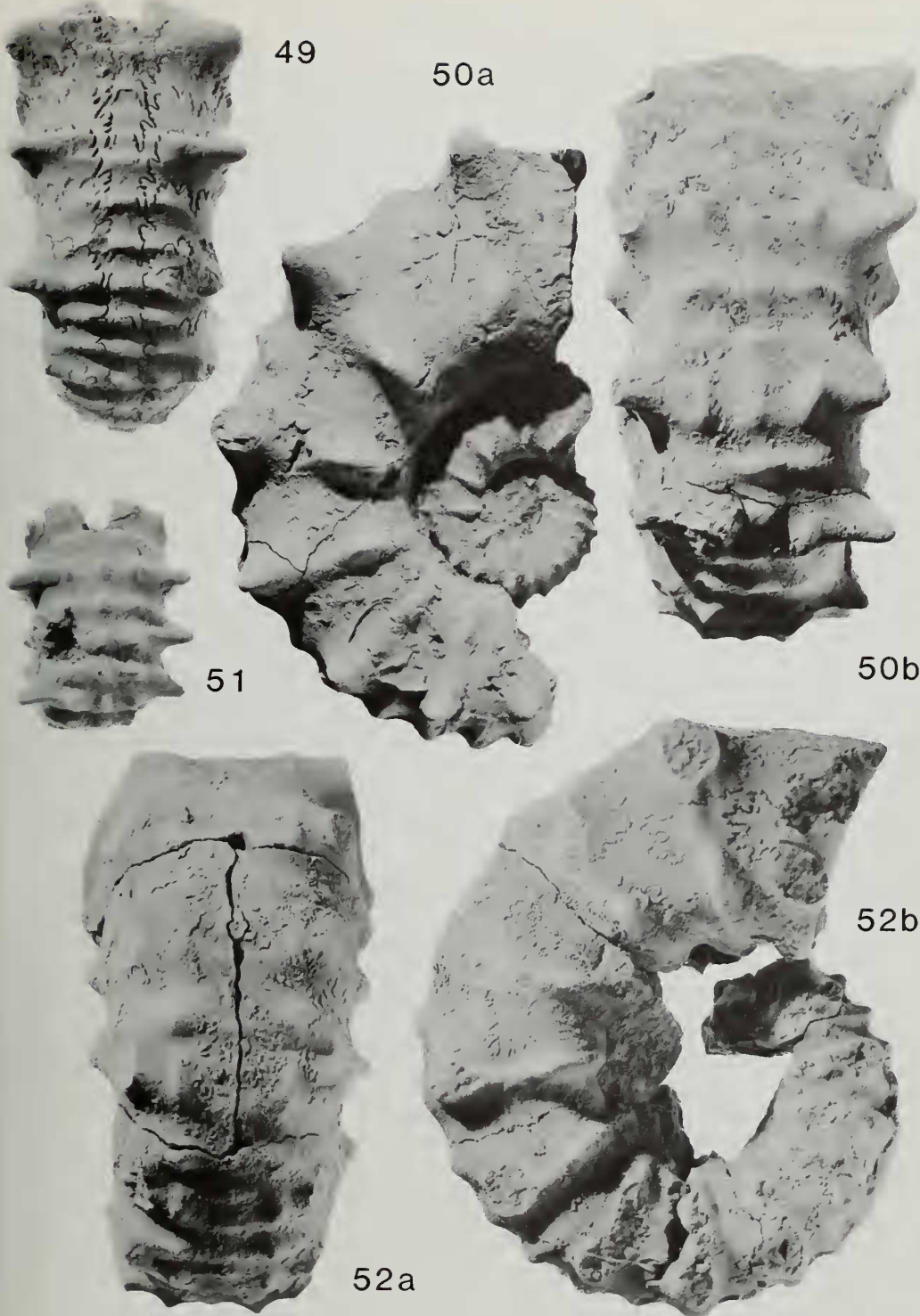


Fig. 47, 48 *Euomphaloceras cunningtoni cunningtoni* (Sharpe). Odukpani Formation (Middle Cenomanian), 28.3 km from Calabar. Fig. 47a–c, C.83100, $\times 1$. Fig. 48a, b, C.83431, $\times 1$. See also Figs 49–52.



Figs 49–52 *Euomphaloceras cunningtoni cunningtoni* (Sharpe). Odukpani Formation (Middle Cenomanian), 28.3 km from Calabar. Fig. 49, C.83440, $\times 1$. Fig. 50a, b, C.83099, $\times 1$. Fig. 51, C.83444, $\times 1$. Fig. 52a, b, C83437, $\times 1$. See also Figs 47, 48.

each rib carries a bullate, rounded umbilical tubercle and a pointed inner ventrolateral tubercle which predominantly extends laterally or ventrolaterally and becomes increasingly prominent as growth proceeds. The major ribs may pass transversely over the venter, or bifurcate in a more or less obvious manner. This usually occurs at the inner ventrolateral tubercles, but sometimes at the outer ventrolaterals. Each of these ventral ribs normally carries a pair of variably pronounced outer ventrolateral tubercles (except when bifurcation occurs here) and a rounded or clavate siphonal tubercle. There are often intercalated minor ventral ribs present as well, each of which may bear a siphonal and a pair of outer ventrolateral tubercles, although frequently the siphonal tubercle occurs in isolation or with only low indefinite outer ventrolateral tubercles. In rare cases, these intercalated ribs also include a pair of low inner ventrolateral tubercles. Asymmetry is common owing to the displacement of siphonal tubercles from the mid-line or to the absence or displacement of one of the inner or outer ventrolateral tubercles. In some individuals there is a regular alternation of a non-bifurcating major rib and a single minor rib. In others there are bifurcating major ribs alternating with one or two minor ribs or isolated siphonal tubercles. Consequently, there are two to four siphonal tubercles to each pair of inner ventrolaterals. The outer ventrolateral tubercles may be rounded or markedly clavate. In the latter cases each corresponds to two siphonal tubercles. The minor ribs may be transverse or convexly curved.

Minor ribs rarely occur at diameters in excess of 60 to 80 mm. When persistent, they tend to be markedly convex or appear only as a siphonal swelling. The tendency towards bifurcation of the major ribs over the venter decreases at this stage. The inner and outer ventrolateral tubercles fuse at large diameters, usually forming a bituberculate horn. There is, normally, a siphonal depression between the horns although they may fuse across the venter. The horns vary in shape, extending predominantly laterally or ventrolaterally and sometimes enlarging dorsally to absorb the umbilical tubercle, so forming a wing-like structure. In large specimens asymmetry is again common owing to abnormalities in the ornament. Often one of a pair of ventrolateral horns is absent or displaced, its associated rib running obliquely across the venter and dying out before reaching the opposite ventrolateral shoulder.

The suture is fairly simple with a moderately deep E, a large bifid E/L and a fairly narrow simple L.

REMARKS. Although this population is highly variable, its mean structure is closest to that in *Euomphaloceras cunningtoni cunningtoni* (Sharpe), the holotype of which was redescribed and figured by Kennedy (1971: 92; pl. 60). In particular, siphonal tubercles outnumber both inner and outer ventrolaterals and large bituberculate horns develop towards adulthood. In the holotype the outer ventrolateral tubercles are markedly clavate, each corresponding to two siphonal tubercles. Many of the present specimens show this pattern, either consistently or in places. It is, however, by no means universal amongst the population as a whole. The present material indicates that Wright (1963: 608) was correct in allowing little weight to minor details of the ventral ornamentation in the *E. cunningtoni* group. Certain individuals in this collection could be placed with some confidence in *E. cunningtoni meridionale* if found alone, showing that overall population structure is a matter of importance here.

In their adult stages the Nigerian specimens commonly display large bituberculate horns, as do the holotype of *E. cunningtoni cunningtoni* and other large individuals (see, for example, Kossmat 1897: pl. 5, figs 1a-c; Kennedy 1971: pl. 61, fig. 2). Thomel (1972: 163), however, described specimens from southern France in which bituberculate horns give way, at diameters in excess of 150 mm or so, to a ribbed ornament with only feeble swellings at the level of the ventrolateral tubercles. A similar adult ornament exists in the Nigerian material referred to *E. cunningtoni meridionale*, above. The question arises, is this a normal ornament for adults in the *E. cunningtoni* group, or is there some variation in this feature, stratigraphic or otherwise? As far as the Nigerian material is concerned, the earliest member of the group (*E. cunningtoni meridionale*) lacks prominent tubercles in the adult while the

later members (*E. cunningtoni cunningtoni* and *E. cunningtoni alatum*) show increasingly massive ventrolateral horns, suggesting that changes in these features are correlated with stratigraphical age differences.

Amongst the present specimens are individuals with whorls higher than broad and others with a predominantly one to one alternation of major and minor ribs. In these respects they resemble *E. lonsdalei* (Adkins 1928, Stephenson 1955, Wright 1963). This morphological overlap demonstrates that, as mentioned above, *E. lonsdalei* is best considered as a subspecies of *E. cunningtoni*.

The difficulties involved in the determination of members of this group have been mentioned above. The majority of previously described specimens, however, appear to fall within the range of *E. cunningtoni cunningtoni* as it is conceived here. Apart from the holotype, the specimens figured by Pictet (1863: pl. 5, figs 2a-c), Kossmat (1897: pl. 5, figs 1a-c), Pervinqui re (1907: pl. 15, figs 1a-c), Erni (1944: pl. 11), Stephenson (1952: pl. 47, fig. 5; pl. 48, figs 3, 4), Wright (1963: pl. 88, fig. 2; pl. 89, fig. 1), Kennedy (1971: pl. 61, figs 2a, 2b) and Wiedmann & Kauffman (1978: pl. 5, fig. 5) all seem to belong here. Specimens from Angola described by Cooper (1973: 61; figs 10A, 10B, 11, 12A, 12B, 13A; 1978a: fig. 8) as *E. cunningtoni meridionale* sometimes show isolated siphonal tubercles and in this respect appear closer to the Nigerian material of *E. cunningtoni cunningtoni*.

Euomphaloceras cunningtoni alatum subsp. nov.

Figs 53-56

HOLOTYPE. C.83479, portions of an adult and a middle whorl (Fig. 53a-c) from the Odukpani Formation (Middle Cenomanian), 30.3 km from Calabar.

PARATYPES. Sixteen specimens (C.83108-12, C.83480-5, UIN 485.1-5), all from the same locality as the holotype.

OTHER MATERIAL. Two further specimens (C.85247, UIN 486.1) from the Odukpani Formation (Middle Cenomanian), 32.2 km from Calabar probably also belong here.

NAME. From the wing-like horns developed in adults.

DIAGNOSIS. *Euomphaloceras* of the *E. cunningtoni* group, distinguished by the typical intercalation of a single minor rib with each major rib in the early and middle stages and by the development of massive wing-like extensions enveloping the whorl sides and outer part of the venter in the adult.

DIMENSIONS.	D	Wb	Wh	U
C.83484	80	44 (55)	35 (44)	31 (39)
C.83108	70	36 (51.4)	—	27 (38.6)

DESCRIPTION. The shell is evolute, the whorls usually being distinctly broader than high with the flanks and the venter rather flattened. The maximum diameter attained is about 200 mm.

Up to a diameter of about 10 mm the flanks are smooth. At this point narrow, rounded, unevenly-developed prorsiradiate ribs appear carrying uneven, often highly effaced umbilical tubercles and more pronounced inner ventrolateral tubercles. The venter is not seen at this stage. By a diameter of 25 mm, the ribs are rectiradiate with definite umbilical tubercles; even at this early stage the inner ventrolateral tubercles are decidedly spinose, the dorsum of the succeeding whorl being notched for their reception. Each major rib also bears a pair of rounded to clavate outer ventrolateral tubercles and a siphonal tubercle. Alternating with each major rib over the venter is a single, short, ventral rib carrying identical outer ventrolateral and siphonal tubercles. At first, however, this alternation of major and minor ribs is not so regular.

Between diameters of 30 and 80 mm there are approximately 13 major ribs in each whorl. They are narrow and rounded, bearing on the flank a prominent bullate umbilical tubercle centred a little outside the umbilical shoulder, and a highly spinose inner ventrolateral

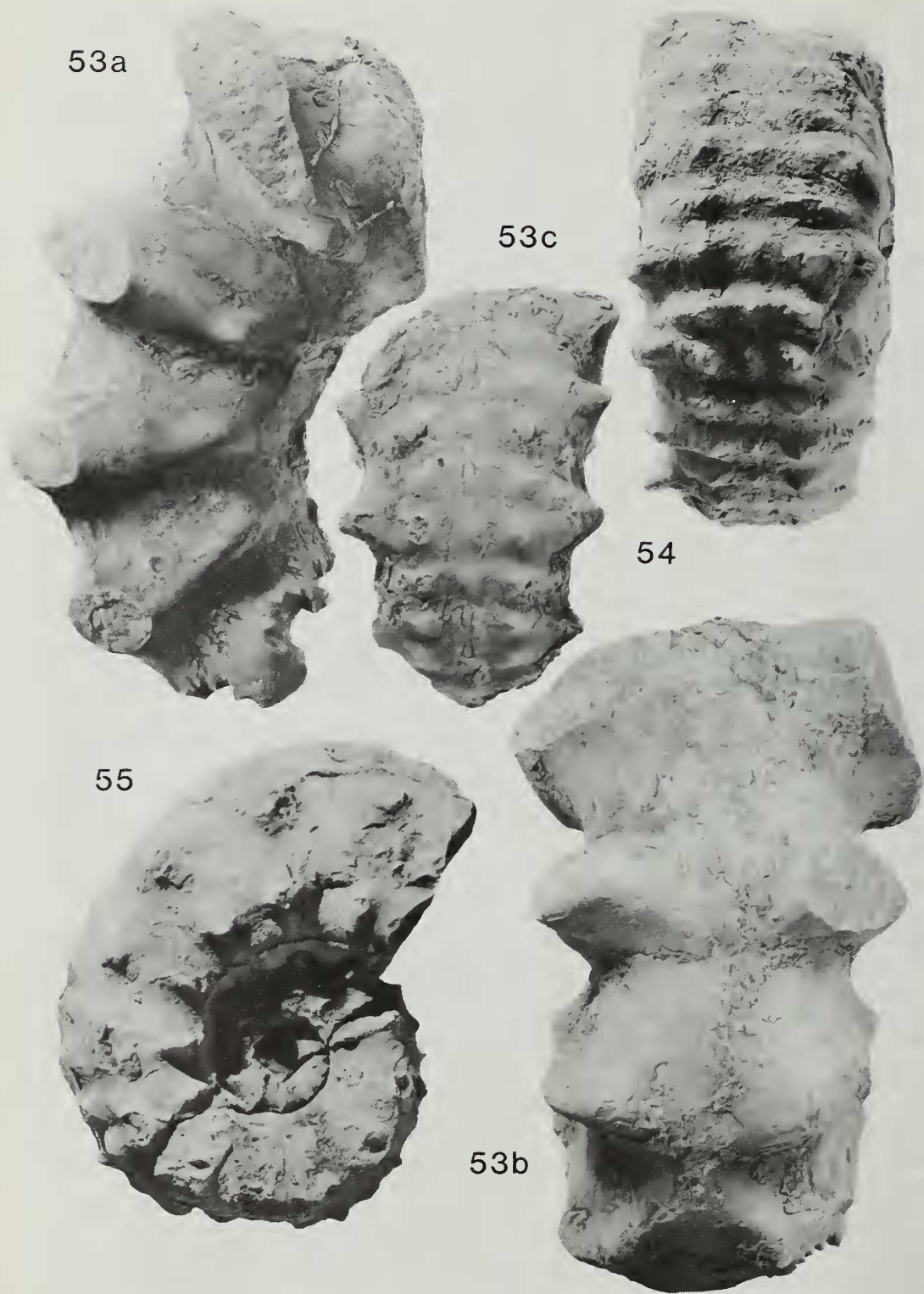
53a

53c

54

55

53b



tubercle. The ribs continue over the venter where they may be transverse or slightly convex. Here each carries a pair of prominent, rounded, conical or clavate outer ventrolateral tubercles and a weaker rounded siphonal tubercle. As growth proceeds the siphonal tubercle becomes progressively weaker. In six (C.83108, C.83481–4, UIN 485.1) of the seven specimens in which this feature is displayed, a single minor rib alternates with each major rib over the venter. In the remaining specimen, the holotype (C.83479), the major ribs bifurcate over the venter and there may be a further rib intercalated with these pairs. Each minor rib carries a pair of outer ventrolateral and a siphonal tubercle developed to exactly the same degree as those of the major ribs. The ventral ribs are commonly convexly curved.

At diameters in excess of 80 mm, the outer ventrolateral and siphonal tubercles and the minor ribs become progressively weaker and, by a whorl height of some 50 mm (diameter approximately 125 mm) they are barely noticeable. At this stage the umbilical tubercles are enlarged and joined to the inner ventrolaterals by broad, rounded ribs. The inner ventrolateral tubercles now become enlarged into horn-like structures. As growth proceeds to full size, all trace of the minor ribs disappears. The ventrolateral horns continue to enlarge, at first assuming a pyramidal shape and finally becoming expanded into narrow wing-like structures enveloping the whorl sides and absorbing the umbilical tubercles. They extend onto the outer part of the venter but there is usually a siphonal depression centrally. The 'wings' may be roughly triangular or pentagonal in shape, extending predominantly laterally or ventrolaterally.

The suture has a deep E, a large deeply bifid E/L and a deep L divided by two elements in the middle stages, but in the adult the suture may be much simplified, L being shallow and broad.

REMARKS. Certain adults in the Nigerian population of *E. cunningtoni cunningtoni*, described above, develop an ornament rather similar to that of *E. cunningtoni alatum* with wing-like ventrolateral extensions, but this character is more pronounced and consistent in the latter subspecies. These two forms also overlap in the details of their ventral ribbing in the early and middle stages; mean population structure is, however, quite different, *E. cunningtoni alatum* only rarely showing more than a single extra ventral rib. As mentioned above these differences seem to be age-related.

E. asura Matsumoto & Muramoto (Matsumoto *et al.* 1969: 277; pl. 35, fig. 1; pl. 36, fig. 1), which according to Kennedy & Hancock (1977: 136) is a junior synonym of *E. multicostatum* (Basse 1940: 446), also develops prominent adult ventrolateral tubercles, but these are much more spinose than in the present material. *E. lehmanni* Collignon (1966: 28; pl. 13, fig. 1) shows a regular alternation of long and short ribs in its middle stages – the adult is unknown – and may be closely related to *E. cunningtoni alatum*. It is, however, rather more densely ribbed. Certain of the horned acanthoceratids of the western interior of the U.S.A. develop a wing-like ornament, for example *Acanthoceras amphibolum* Morrow and *A. muldoonense* Cobban & Scott (see Cobban & Scott 1972), but their early and middle stages are quite different and they are not closely related to the present material.

Genus *KAMERUNOCERAS* Reyment, 1954a

TYPE SPECIES. *Acanthoceras eschii* Solger, 1904; by the original designation of Reyment, 1954a.

Kamerunoceras tinrhertense Collignon, 1965 Figs 57–59

1965 *Kamerunoceras tinrhertense* Collignon: 175; pl. D.

Figs 53–55 *Euomphaloceras cunningtoni alatum* subsp. nov. Odukpani Formation (Middle Cenomanian), 30.3 km from Calabar. Fig. 53a–c, **holotype** C.83479: Fig. 53a, b show outer whorls $\times 0.65$, Fig. 53c shows ventral view of the preceding whorl $\times 1$. Fig. 54, paratype C.83108 in ventral view, $\times 1$. Fig. 55, paratype C.83484, $\times 1$. See also Fig. 56.

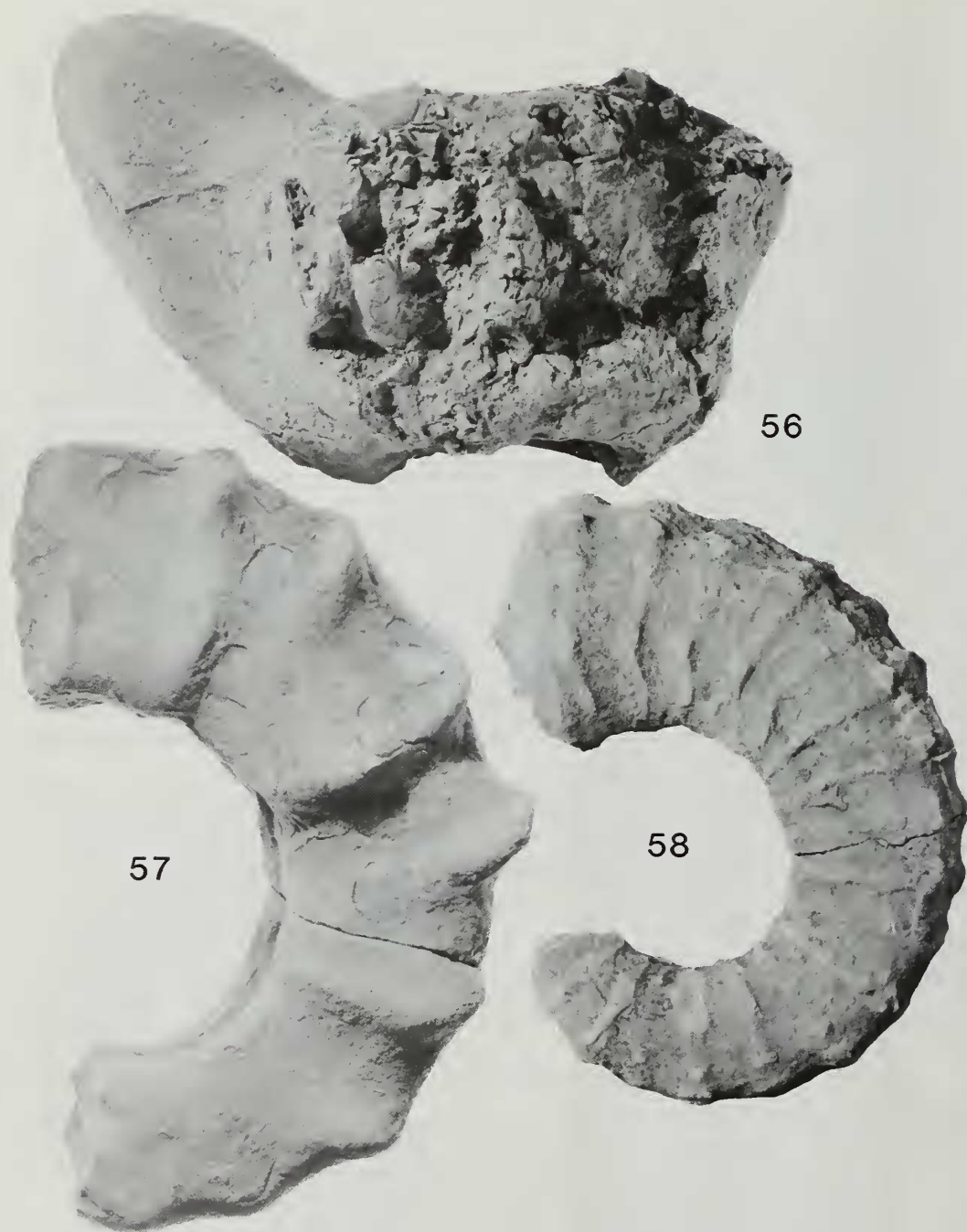


Fig. 56 *Euomphaloceras cunningtoni alatum* subsp. nov. Odukpani Formation (Middle Cenomanian), 30.3 km from Calabar. Paratype C.83111, $\times 1$, apertural view showing adult ventrolateral ornament. See also Figs 53–55.

Figs 57, 58 *Kamerunoceras tunrhertense* Collignon. Odukpani Formation (Lower Turonian), 34 km from Calabar. Fig. 57, C.83489, $\times 0.65$. Fig. 58, C.83493, $\times 0.75$. See also Fig. 59.

MATERIAL AND OCCURRENCE. Twenty-one specimens (C.83126-7, C.83489-94, UIN 426.1-13) from the Odukpani Formation (Lower Turonian), 34 km from Calabar.

DESCRIPTION. The shell is very evolute and reaches a diameter of at least 200 mm. The whorls are rectangular being slightly to distinctly higher than broad.

The earliest whorls are not seen. Between diameters of about 70 and 110 mm there is considerable variation in ornamentation, the number of ribs varying between extremes of 24 and about 40 to a whorl. Most ribs are long and narrow, each with a rounded to bullate umbilical tubercle and a pair of inner and outer ventrolateral tubercles. There are also clavate siphonal tubercles tending to form an intermittent keel. On some of the ribs the umbilical tubercles are markedly effaced and often absent altogether, these ribs being confined to the ventral part of the flank. In some specimens there is a fairly regular alternation of long and short ribs. The umbilical tubercles tend to migrate ventrally towards the mid-flank region during ontogeny and often a further tubercle develops on the umbilical shoulder. The ribs may be prorsiradiate between these pairs of umbilical tubercles and somewhat rursiradiate to rectiradiate on the ventral part of the flank.

As growth proceeds, the siphonal and outer ventrolateral tubercles fade and finally disappear while the inner ventrolaterals enlarge markedly. The umbilical tubercles swell into large bullate structures occupying the whole of the dorsal half of the whorl sides. The ribs become broader and more widely spaced at large diameters. In the adult whorl there are only 14-15 ventrolateral tubercles and fewer umbilical tubercles. In some cases each umbilical tubercle may correspond in a regular fashion to two ventrolaterals, while in others the umbilical tubercles are more numerous but sporadically distributed. At adulthood the ventrolateral tubercles may tend to fuse across the venter.

The suture is simple with a narrow E, a broad bifid E/L, a rather narrow L, a simple asymmetrically bifid L/U₂ and a narrow shallow U₂.

REMARKS. *Kamerunoceras tinrhertense* Collignon (1965: 175; pl. D) is based upon a single wind-worn specimen from the Lower Turonian of the Algerian Sahara, and knowledge of its morphology and individual variation is therefore incomplete. It is clear, however, that the present material agrees with this species in important aspects of its morphology and ontogeny as well as in its large size. In particular the ribbing is dense in the early stages, while at adulthood there are coarsely ornamented, distant ribs. Ventrolateral tubercles outnumber umbilicals throughout middle and late ontogeny.

In their middle growth stages the present specimens may show approximately the same rib density as *K. turoniense* (d'Orbigny) and those variants with few intercalated ribs rather resemble that species at this stage (see Fig. 58; Kennedy & Wright 1979: pl. 3, fig. 1). In addition both show duplication of the umbilical tubercles (see above; Pervinquière 1907: pl. 19, fig. A; Kennedy & Wright 1979: 1174). *K. turoniense*, however, has more distant ribs in its early stages, dense weaker ribbing in the adult, and also lacks intercalated ribs.

Rather similar to the present material in general shape and suture pattern, and in showing long and short ribs with duplication of the umbilical tubercles, is *Polyaspidoceras shimizui* Matsumoto (Matsumoto, Kawashita, Fujishima & Miyauchi 1978: 21, fig. 7). This form, however, possesses yet another extra row of tubercles on the flank. This species was made the basis of the new genus *Polyaspidoceras* but it is questionable whether it is separable from *Kamerunoceras*.

Probably conspecific with the present material are specimens collected in the Odukpani Formation a little to the east of the present road section and referred by Fayose (1977: 237, fig. 4) to *Hoplitoides crassicosatus* Reymont.

Family COILOPOCERATIDAE Hyatt, 1903

Genus COILOPOCERAS Hyatt, 1903

TYPE SPECIES. *Coilopoceras colleti* Hyatt, 1903; by original designation.

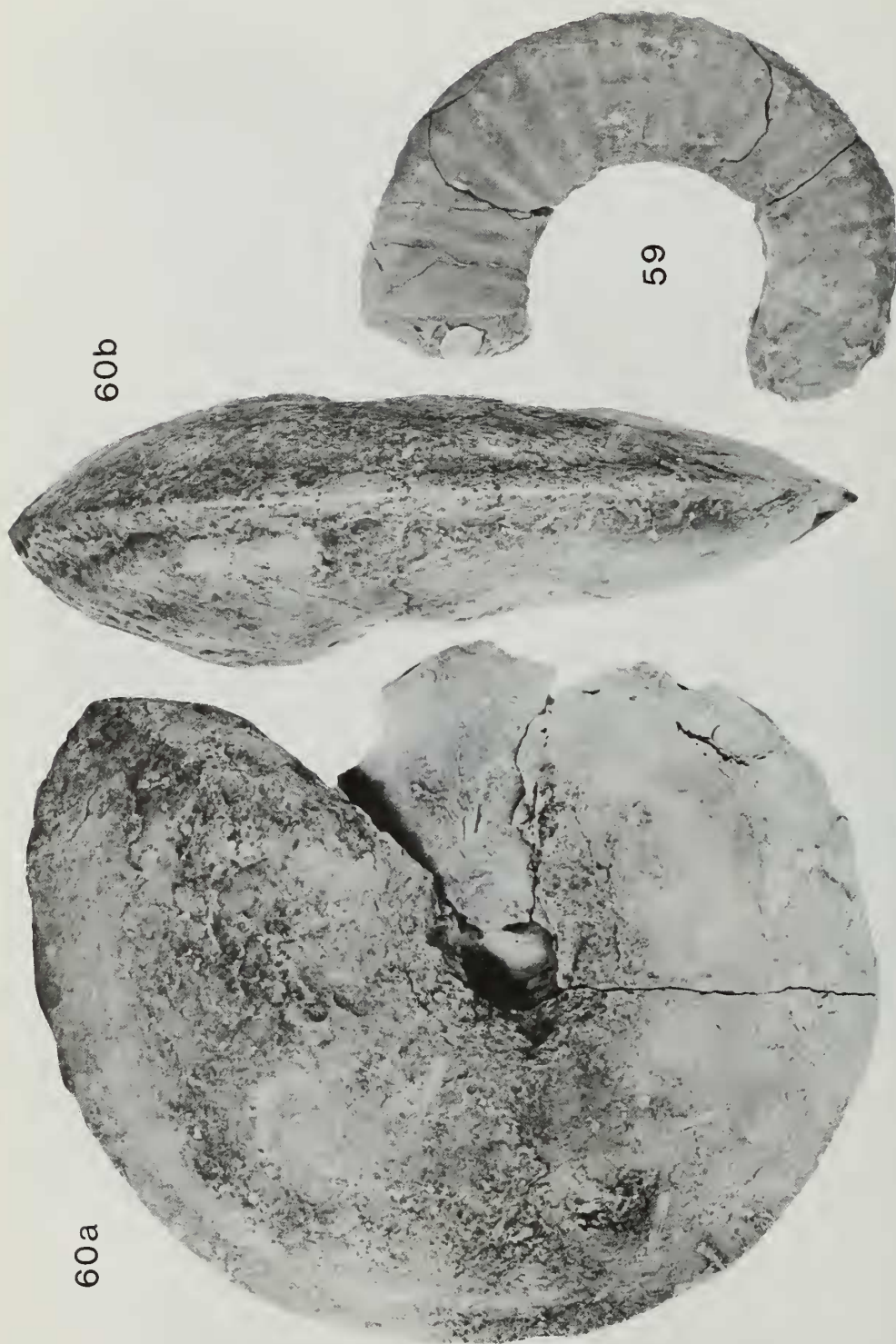


Fig. 59 *Kamerunoceras tinrherdense* Collignon. Odukpani Formation (Lower Turonian), 34 km from Calabar. C.83494, $\times 0.75$. See also Figs 57, 58.

Fig. 60a, b *Coilopoceras* aff. *newelli* Benavides-Cáceres. Odukpani Formation (Lower Turonian). 34 km from Calabar. C.83486, $\times 0.65$, a specimen showing average whorl breadth and strength of ornamentation. See also Figs 61, 62.

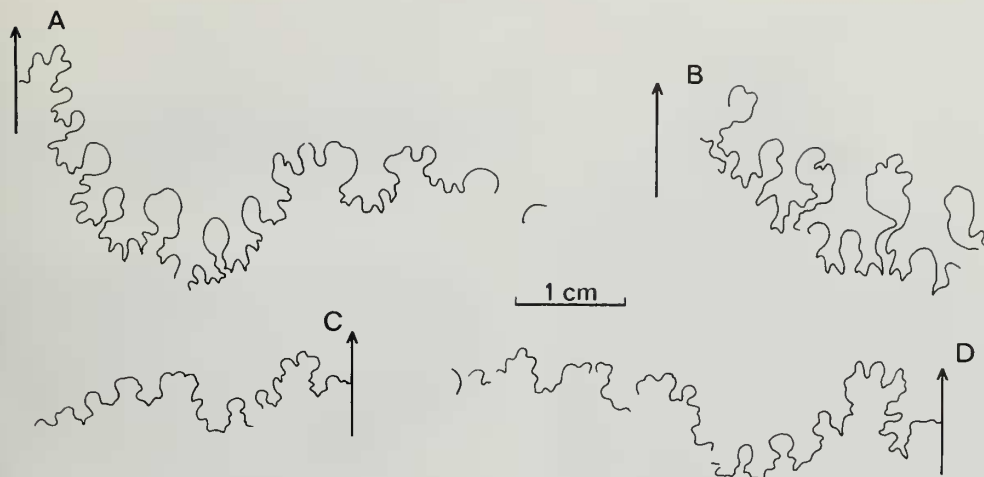


Fig. 61 Sutures in *Coilopoceras* aff. *newelli* Benavides-Cáceres. A, C.83123 at whorl height of 90 mm; B, UIN 427.3; C, C.83124 at whorl height of 60 mm; D, UIN 427.4 at whorl height of 90 mm.

Coilopoceras aff. *newelli* Benavides-Cáceres, 1956
Figs 60–62

Compare: 1956 *Coilopoceras newelli* Benavides-Cáceres: 473; pl. 61, figs 4, 5; pl. 62, figs 5–7.

MATERIAL AND OCCURRENCE. Twenty-nine specimens (C.83121–4, C.83486–8, UIN 427.1–21) from the Odukpani Formation (Lower Turonian), 34 km from Calabar.

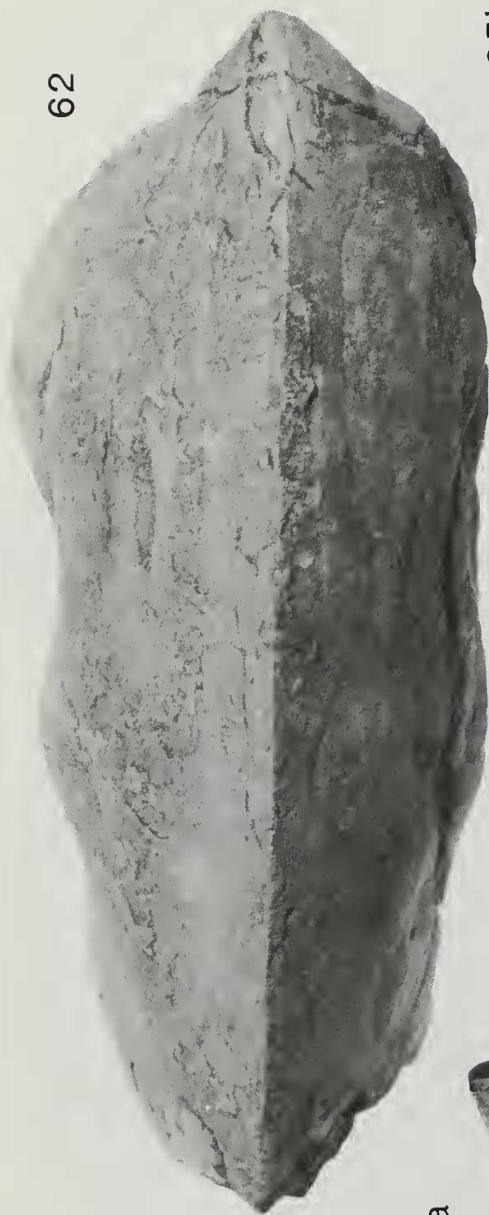
DESCRIPTION. The shell attains a very large diameter, in excess of 500 mm. The umbilicus is tiny in the early stages but widens slightly later on. The whorl sides are convex, converging on the sharp venter. The umbilical shoulders are rounded and indistinct. The siphuncle is wide but constricted at the septal necks. The body chamber is about half a whorl in length.

In the early stages the whorl sides appear smooth, but since the material consists of weathered internal moulds it is unlikely that any fine ornament would be preserved. At a varying stage in ontogeny, but usually by a diameter of about 100 mm, definite ornamentation appears, consisting of broad bulge-like swellings on the flanks. These arise just outside the umbilical shoulder, reach their greatest height just dorsal of the mid-flank region and die out on the ventral part of the flank. There are six or seven bulges in each whorl. Some individuals show a weak ornament of elongate rib-like structures while others remain smooth at diameters in excess of 300 mm. Shell breadth also varies. Some specimens are compressed and tend to have a weak ornament; others rather inflated, in which it is generally more pronounced.

The sutures (Fig. 61) develop a highly sigmoidal pattern. They are variable in their details, sometimes being relatively simple, although the saddles may be elongated with constricted necks and globular endings.

REMARKS. This material is similar to *Coilopoceras newelli* Benavides-Cáceres (1956: 473) from the Turonian of Peru, which also develops broad, elongate swellings at a varying stage in ontogeny. The Peruvian population also includes examples of inflated forms with a pronounced ornament (Benavides-Cáceres 1956: pl. 62, figs 5–7) along with weakly ornamented smooth variants (Benavides-Cáceres 1956: pl. 61, fig 5). The ornament in *C. newelli*, however, seems to be a little more rib-like and there appear to be slightly more of the bulges in each whorl.

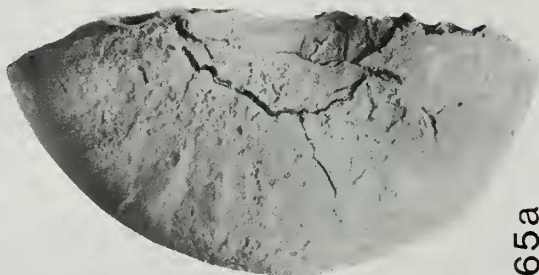
62



65b



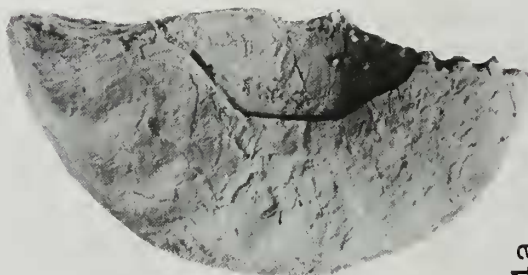
65a



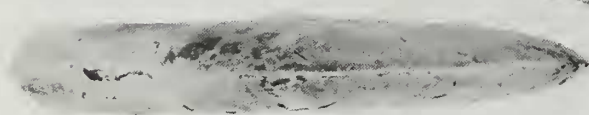
64b



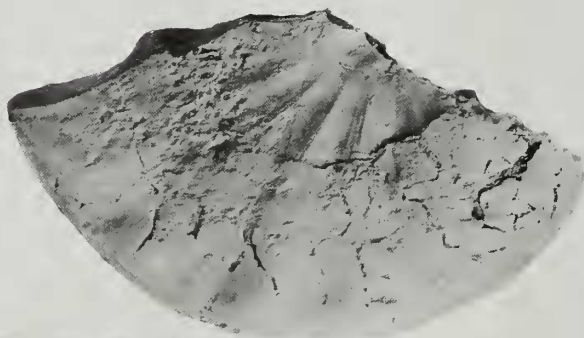
64a



63a



63b



C. colleti Hyatt and *C. inflatum* Cobban & Hook from the middle part of the Turonian in the western interior of the U.S.A. (see Cobban & Hook 1980) are also similar to the present material. At large diameters *C. colleti* develops prominent lateral swellings (Cobban & Hook 1980: pl. 8; pl. 9; text-fig. 9) but these extend further ventrally than in the Nigerian material and this species also shows ventrolateral tubercles and ribbing in the early stages. *C. inflatum* develops an even more inflated adult shell (Cobban & Hook 1980: pl. 13) and its bulge-like ornament envelops more or less the whole of the whorl sides. *C. inflatum* also includes inflated, grossly ornamented variants and compressed smooth forms. Cobban & Hook (1980) interpreted the two varieties as dimorphs, the stouter forms sometimes dominating the population while at other localities there occur more even mixtures of the two types. This type of variable population structure thus seems to be common in *Coilopoceras*, but there seems to be no clear distinction between the two groups in the Nigerian material; rather they intergrade into one another.

Another highly inflated species is *C. discoideum* Barber (1957: 55; pl. 2, fig. 1; pl. 3, figs 1, 2; pl. 25, figs 1–4) but its ornament is stronger in the early whorls, the ribs broadening and disappearing in the adult stages.

Closely similar to the stout, grossly ornamented variants in *Coilopoceras* is the genus *Glebosoceras* Reymont (type species *Glebosoceras glebosum* Reymont 1954: 161; pl. 2, fig. 3; pl. 4, fig. 1). *Glebosoceras* also shows an ornament of broad bulge-like ribs and there seems to be little justification in separating it from *Coilopoceras*.

Fayose (1977: 235, fig. 5) described specimens from the Odukpani Formation as *Hoplitoides ingens* (von Koenen). These also show the bulbous ornament characterizing the present material and may be conspecific.

Family SPHENODISCIDAE Hyatt, 1900

Genus SPHENODISCUS Meek, 1871

TYPE SPECIES. *Ammonites lobata* Tuomey, 1856 (= *A. lenticularis* Owen, 1852 *non* Young & Bird, 1828); by the original designation of Meek, 1871.

Sphenodiscus lobatus (Tuomey) *costatus* Zaborski, 1982 Figs 63–65

1982 *Sphenodiscus lobatus costatus* Zaborski: 320, figs 22, 23, 26–35.

MATERIAL AND OCCURRENCE. A total of 262 specimens from the upper Nkporo Shale (Lower Maastrichtian), 42 km from Calabar. In addition to the material listed by Zaborski (1982: 320) these include UIN 424.156–201 and C.85270–5.

REMARKS. This subspecies was described by Zaborski (1982: 320). The material considered included a number of small individuals showing variation in venter shape and ornamentation. These differences were thought to represent individual variation but further collections suggest the existence of dimorphism in this form.

The majority of the specimens from the locality reach a large diameter, in excess of 200 mm. A number were figured by Zaborski (1982: figs 23, 26–34). Others, preserved at a smaller diameter, represent the inner whorls of such large specimens (see Zaborski 1982: fig. 35). A few individuals seem to represent a second group, but only six (C.83185, C.83188,

Fig. 62 *Coilopoceras* aff. *newelli* Benavides-Cáceres. Odukpani Formation (Lower Turonian), 34 km from Calabar. C.83520, $\times 0.75$, ventral view of a fairly broad, grossly ornamented variant. See also Figs 60, 61.

Figs 63–65 *Sphenodiscus lobatus costatus* Zaborski. Upper Nkporo Shale (Lower Maastrichtian), 42 km from Calabar. Fig. 63a,b, C.85273, $\times 1$. Fig. 64a,b, C.85271, $\times 1$. Both are microconchs(?) showing early broadening of the venter and development of ornament on the whorl sides. Fig. 65a,b, C.85275, a possible microconch(?), $\times 1$.

C.83190, C.85271, C.85273–4) can be placed in it with confidence. They reach a maximum diameter of 75–80 mm but, since they consist exclusively of internal moulds of the body chamber alone, adulthood cannot be demonstrated on the basis of sutural simplification or approximation. At diameters in excess of 40–50 mm the initially sharp venter broadens and becomes fastigiate with a definite keel evident, or becomes broadly rounded. Broad, bullate rib-like structures develop; they are most pronounced ventrally and usually expanded into prominent ventrolateral tubercles. Although adulthood cannot be proved, it is possible that these specimens represent the microconch of this subspecies. The macroconch(?) retains a sharp venter and smooth flanks to a late stage in ontogeny (Zaborski 1982: 322).

Some problematical specimens show intermediate characters (see Zaborski 1982: fig. 22; Fig. 65a,b). They may represent microconchs(?) with a relatively narrow venter or alternatively some of the macroconchs(?) may show a subdued ornament in their early growth stages.

Dimorphism has previously been unknown in *Sphenodiscus*. *S. pleurisepta* (Conrad) develops pronounced ornamentation (Hyatt 1903: pl. 3, figs 7–15; pl. 4, figs 1, 2; pl. 5, figs 1–3; pl. 6, fig. 6), as does the related genus *Coahuilites* Böse (1927: 279), which shows a broad venter in its later growth stages. Both, however, reach a considerably larger size than the microconchs(?) described here.

Correlation and palaeogeography

Until the creation of the roadside cuttings described here, knowledge of the Cenomanian in southern Nigeria had been rudimentary. Reyment (1956, 1965), however, attempted a broad biostratigraphic subdivision of the Nigerian Cenomanian based upon ammonites. He proposed two zones: a lower 'Zone of *Euhystrihoceras occidentale* Reyment' containing, in addition to the nominal species, *Desmoceras* (*Pseudouhligella*) *calabarensis* Reyment, *D. (D.) latidorsatum* (Michelin) and *Phylloceras* cf. *velledae* (Michelin); and an upper 'Zone of *Turrilites scheuchzerianus*' also containing *T. costatus*, *Forbesiceras sculptum* Crick, *F. aff. conlini* Stephenson, *Acompsoceras subwaterloti* Venzo, *Acanthoceras quadratum nigeriense* Reyment, *Calycoceras*, *Metoicoceras* and *Sharpeiceras*. The presence of *Euhystrihoceras* suggests a Lower Cenomanian age for his lower zone (see review of this genus in Kennedy & Wright 1981), but the upper zone contains forms characteristic of each Cenomanian substage. The existence of the Lower Cenomanian was confirmed by Förster (1978) and Förster & Scholz (1979), who reported basal Cenomanian ammonites in the Mfamosing Quarry just to the east of the present road section (see Fig. 2, p. 5). This quarry works a limestone (= 'Lower Limestone' of Murat (1972: 256); Mfamosing Limestone Formation of Petters (1982)) in the basal part of the Odukpani Formation which locally reaches a thickness of some 100 m. At Mfamosing the limestone is largely without ammonites, but towards the top it yields *Mortoniceras*. The upper surface of the limestone is an eroded hardground with a condensed horizon above containing a mixture of uppermost Albian and Lower Cenomanian ammonites (Förster & Scholz 1979: 111). The upper surface of this limestone can therefore be taken as locally representing the Albian–Cenomanian boundary. Large blocks, the remnants after dissolution of an algal biosparite similar to parts of the Mfamosing limestone, occur in the present road section immediately below the shales yielding fauna 1 described here. These shales can be assigned a definite Lower Cenomanian age on the basis of *Sharpeiceras laticlavium nigeriense*. Correlation with the *Hypoturrilites carcitanensis* or *Mantelliceras saxbii* Zone in southern England is most probable since both contain *S. laticlavium*. Faunas 2 and 3 described here may also be of Lower Cenomanian age. Fauna 2 contains *Puzosia* sp., *Acompsoceras* aff. *renevieri* and another *Acompsoceras* (C.83497) which shows umbilical bullae and a weakly ornamented venter, being close to *A. essendiense* (Schlüter 1871: 3; pl. 1, figs 5–7). Both of these *Acompsoceras* occur in the Lower Cenomanian of southern England (Kennedy 1971, Kennedy & Hancock 1978), although they may range higher. The *Forbesiceras* in fauna 3 is specifically indeterminate and cannot be accurately dated. The full extent and faunal content of the Lower Cenomanian part of the

Odukpani Formation is, therefore, still to be determined and detailed correlation with other areas is not yet possible. Similarly the age of the clastics of the Awi Formation and, indeed, that of the earliest sediments in the Calabar region remains unresolved. There are, however, reports of possible pre-Albian marine sediments in the shallow subsurface close to the Mfamosing Quarry (Ramanathan & Kumaran 1981).

A large part of the present material comes from the Middle Cenomanian portion of the Odukpani Formation and considerably enlarges our knowledge of it. In southern England and northern France the Middle Cenomanian (Zone of *Acanthoceras rhotomagense*) can be divided into three assemblage zones (see Kennedy 1971, Kennedy & Hancock 1977, 1978, Juignet & Kennedy 1976): a lower Zone of *Turrilites costatus*, a middle Zone of *T. acutus* and an upper Zone of *Acanthoceras jukesbrownei*. These horizons have sufficient faunal similarity to the Calabar region to allow detailed correlation. Those parts of the Odukpani Formation containing faunas 4, 5, 8 and 9, described here, correlate with the *costatus* and *acutus* Zones as they have the following species in common: *Turrilites costatus*, *T. acutus*, *T. scheuchzerianus*, *Anagaudryceras involvulum*, *Euomphaloceras inerme*, *E. cunningtoni* and *Forbesiceras obiectum*. The lower beds (with faunas 4 and 5) equate with the *costatus* Zone; the nominal species, *E. inerme* and early members of the *E. cunningtoni* group indicate this zone, probably the top part of it (see Kennedy 1971: 94, 96; Kennedy & Hancock 1977: 135). The Nigerian *E. inerme* often resembles *Acanthoceras rhotomagense* var. *sussexiense*, typical of the *costatus* Zone in north-west France (Kennedy & Hancock 1970). The *T. costatus* in fauna 5 are transitional to *T. acutus*, suggesting a position close to the boundary of the *costatus* and *acutus* Zones. The upper beds (with faunas 8 and 9) seem to equate with the *acutus* Zone. Fauna 8 includes the nominal species and *Forbesiceras obiectum* which occurs in this zone. The material referred here to *Calycoceras annulatum* seems to be most closely related to *Calycoceras* of the *newboldi* group, characteristic of the *acutus* Zone and younger strata in western Europe. In Normandy *Anagaudryceras involvulum* is known only from the *costatus* Zone (Juignet & Kennedy 1976), but its presence in younger strata in the Odukpani Formation is of little consequence, as it appears to have a long range: it has been described from the Turonian of Angola (Howarth 1966). Fauna 9 contains two specimens (C.85247, UIN 486.1) transitional between *Euomphaloceras cunningtoni cunningtoni* and *E. cunningtoni alatum*, but closer to the latter. Their associated *Acanthoceras robustum* suggests correlation with the *acutus* Zone (see p. 35). This fauna is, in fact, very close in age to, though probably slightly older than, fauna 8 of which *E. cunningtoni alatum* is a major element. Its westerly position in the road section is because folding has repeated the strata.

None of the diagnostic species of the European *jukesbrownei* Zone occurs in the Nigerian collection. Instead, the succeeding beds (with fauna 7) in the Calabar section (occurring east of those with fauna 8 as a result of folding) contain *Acanthoceras amphibolum*. This species provides an important point of reference with North American faunas. In the western interior of the U.S.A., *A. amphibolum* is the index for a zone in the upper part of the Middle Cenomanian (Cobban & Scott 1972: table 4; Kauffman *et al.* 1978). It also occurs at one level in the Japanese Middle Cenomanian (Matsumoto, Okada, Hirano & Tanabe 1978: 4; Kennedy & Hancock (1977: 135) tentatively correlated this horizon with the *jukesbrownei* Zone in Europe. The Nigerian sequence suggests that this is indeed correct, the *A. amphibolum* beds here appearing to correlate with the basal part of the *jukesbrownei* Zone. Middle Cenomanian faunas from the western interior have little else in common with Nigeria, only members of the *E. cunningtoni* group inviting immediate comparison. Forms similar to *E. cunningtoni cunningtoni* occur in the oldest undoubted Cenomanian in the western interior, the Thatcher Limestone Member of the Graneros Shale in south-eastern Colorado (Cobban & Scott 1972: 70; pl. 40; Kauffman *et al.* 1978: 11), belonging in the Zone of *Calycoceras* (*Conlinoceras*) *tarrantense* (Adkins). *Turrilites acutus* is also present here. This zone seems to correspond with the upper part of the *costatus* Zone or, more probably, the lower part of the *acutus* Zone in western Europe. The most nearly contemporaneous part of the Odukpani Formation is that yielding fauna 5. Overlying the Zone of *C. tarrantense* in the western interior there is a zone characterized by *Acanthoceras granerosense* below and *A.*

muldoonense above. In Colorado, forms close to *Euomphaloceras cunningtoni lonsdalei* are associated with *A. muldoonense* (Cobban & Scott 1972: pl. 42; Kauffman *et al.* 1978: 11), which seems to be contemporaneous with *E. cunningtoni alatum* in Nigeria. These two forms, both characterized by a reduction in the ventral ribbing and tuberculation, occur only a few metres below horizons with *Acanthoceras amphibolum*. Members of the *E. cunningtoni* group appear, therefore, to have some potential as stratigraphical indicators. In Japan and Texas, however, contradictory successions are reported. In Texas Young & Powell (1978: fig. 5) indicate *E. cunningtoni lonsdalei* appearing before *E. cunningtoni cunningtoni* and both as being at least partly contemporaneous with *A. amphibolum*. In Japan Matsumoto, Okada, Hirano & Tanabe (1978: 4) report *E. cunningtoni meridionale* in association with *A. amphibolum*, although in the Odukpani Formation it occurs considerably below the latter species.

Although faunal confirmation is lacking, structural evidence suggests that the highest Middle Cenomanian in the present section is that containing fauna 6 which occurs close to a synclinal axis. The only stratigraphically useful ammonite found here is *Forbesiceras obtectum*, which ranges through most of the Middle Cenomanian in north-west Europe (Kennedy & Hancock 1977: fig. 3).

Middle Cenomanian faunas from the Cuanza Basin in Angola have much in common with those of the Odukpani Formation. Near Novo Redondo, strata of *costatus* and *acutus* Zone age yield *Turrillites costatus*, *T. acutus*, large *Forbesiceras obtectum*, *Euomphaloceras* of the *cunningtoni* group and *Calycoceras annulatum* (Cooper 1973, 1978a). The Nigerian Middle Cenomanian, however, extends both higher and lower than the Novo Redondo beds. Thus *Euomphaloceras inerme* is unknown in the latter and the Angolan *E. cunningtoni* appears to be closer to the Nigerian *E. cunningtoni cunningtoni* than to the earlier *E. cunningtoni meridionale*. *Acanthoceras* cf. *granerosense* occurs at Novo Redondo (Cooper 1978a: 6), indicating beds older than the horizon with *A. amphibolum* in Nigeria. Lower Cenomanian occurs in the Novo Redondo area but, as in Nigeria, it is not sufficiently understood for detailed comparison. *Sharpeiceras laticlavium* (= *S. goliath* Haas) occurs east of Luanda (Haas 1942, Cooper 1978a: 6).

The Nigerian Cenomanian ammonites act as a palaeobiogeographical link between west European and Angolan faunas. According to Reyment & Tait (1972), the final opening of the South Atlantic Ocean, allowing free north-south faunal migration, took place as late as the end of the Lower Turonian. Kennedy & Cooper (1975), Kennedy & Cobban (1977: 76-80), Cooper (1978: 144-145), Förster (1978) and Förster & Scholz (1979) all presented evidence, based on ammonite distributions, to show that continuous migration was possible from late Albian times onwards. The present material strongly suggests that such migration took place during the Cenomanian. Particular mention may be made of *Acanthoceras amphibolum* and *Puzosia* (*Anapuzosia*) *dibleyi*. *A. amphibolum* is most typical of Texas and the western interior of the United States, otherwise occurring only in Japan and perhaps southern England. Its presence in southern Nigeria is difficult to explain unless migration from the North Atlantic was possible. *P. (A.) dibleyi* is known only from Angola and southern England. The presence of a very similar form in Nigeria, albeit in earlier strata, also suggests linkage.

Structural and faunal evidence suggests that an unconformity separates Middle Cenomanian from younger strata in the Odukpani Formation. Beds above this unconformity seem to dip uniformly to the south-west, those below are broadly folded. The youngest parts of the Middle Cenomanian and much of the Upper Cenomanian appear to be missing. The only Upper Cenomanian ammonite in the present collection is *Pseudocalyoceras* cf. *haughi*, but unfortunately the exact position of this specimen in the road section is uncertain. Reyment (1955: 47) described *Metoicoceras* aff. *ornatum* Moreman (= *M. geslinianum* (d'Orbigny): see review of this species in Kennedy *et al.* 1981: 60-76) from the Odukpani Formation, indicating the presence of terminal Cenomanian. This species is an important element of the *Sciponoceras gracile* faunal assemblage, which is recognizable almost world-wide (see Cooper 1978: 142-144). It would indeed be surprising if this assemblage were absent

altogether, since one of its members, *Euomphaloceras septemseriatum*, occurs in the middle Benue Valley of central Nigeria (Offodile 1976, Offodile & Reyment 1976). But whether the *Pseudocalycoceras* from the Odukpani Formation is also of *S. gracile* Zone age is unproved; the sediments directly above the unconformity are not younger than this, which was a time of eustatic sea level rise and so a plausible date for the re-commencement of sedimentation. Nwachukwu (1972) and Olade (1975) also presented evidence for an intra-Cenomanian folding phase in southern Nigeria. Low dips occur in the Calabar region, but the Albian sediments outcropping in central south-eastern Nigeria are more strongly deformed, dips approaching the vertical being common. Although the intensity of the deformation is partly due to a later Santonian–Campanian tectonic episode, the possibility remains that marine Lower and Middle Cenomanian was removed from parts of southern Nigeria during the late Cenomanian folding.

The limestones in the uppermost part of the Odukpani Formation with *Kamerunoceras tinrhertense* and *Coilopoceras* aff. *newelli* are probably Lower Turonian. In Algeria *K. tinrhertense* is well dated as Lower Turonian (Collignon 1965: 198–199). Although *C. newelli* occurs in the upper part of the Turonian in Peru (Benavides-Cáceres 1956) and the related species *C. colleti* and *C. inflatum* are of mid and early late-Turonian age respectively in the United States (Cobban & Hook 1980), evidence from northern Nigeria (Barber 1957: 59, 61) indicates that *Coilopoceras* begins its range low in the Turonian and possibly even in the high Cenomanian. The Lower Turonian part of the Odukpani Formation is sometimes (see, for example, Petters 1980, 1982) referred to the Eze-Aku Formation. There is no real lithostratigraphic justification for this, however, and Reyment's (1955) original practice of including these strata in the Odukpani Formation is followed here.

Reyment (1956, 1965) divided the Nigerian Maastrichtian into three zones, from bottom to top: the Zone of *Libycoceras afikpoense* Reyment; the Zone of *Sphenodiscus studeri* Reyment; and the Zone of *Cordiceramus coxi* (Reyment). The Zone of *L. afikpoense* is, in fact, of Upper Campanian age but this species is an excellent indicator of the earliest marine Campanian in Nigeria. Reyment's upper two zones are unsatisfactory and, although said to be of Upper Maastrichtian age, they are not accurately dated and are almost certainly older.

The basal Nkporo Shale in the Calabar region falls into the Zone of *L. afikpoense*. The closest relative of this species, *L. ismaelis* (Zittel), begins its range in the lower part of the Zone of *Bostrychoceras polyplacum* in the Middle East (Reiss 1962). Like *L. afikpoense*, *L. ismaelis* occurs in association with *Sphenodiscus lobatus* (Picard 1929, Lewy 1977, Zaborski 1982) and a similar Upper Campanian age is most likely for the Nigerian species. None of the associated ammonites in the basal Nkporo Shale rules out an Upper Campanian age. *Pachydiscus egertoni* is said to be confined to the Campanian part of the Ariyalur Group in India (Sastri *et al.* 1968). The closely similar *P. neubergicus*, often considered to be a synonym of *P. egertoni* (see Matsumoto 1959: 43–44), is, however, an index for the Lower Maastrichtian in western Europe (Jeletzky 1951), although it may range both higher and lower (see Hancock & Kennedy 1981: 544). *Didymoceras cheyennense* (and indeed all the large *Didymoceras* of the western interior of the U.S.A.) occurs in the high Campanian (Gill & Cobban 1973: table 1; text-fig. 12). Along the Pacific coast of North America *D. hornbyense* and its allies are either of late Campanian or early Maastrichtian age (Usher 1952, Anderson 1958, Jones 1963). *Pseudoxybeloceras* (*Parasolenoceras*) occurs at various levels in the Campanian, typically being older than Upper Campanian (Matsumoto 1959: 164; Collignon 1969: 44, 47; Ward & Mallory 1977). *Gaudryceras varicostatum* ranges in age from Coniacian to Campanian (Kennedy & Klinger 1979: 138). Finally, Reyment (1955: 15) reported '*Bostrychoceras*' in the *Libycoceras afikpoense* Zone in south-east Nigeria. Thus the weight of evidence points to an Upper Campanian (*polyplacum* Zone) age for this horizon.

The overlying beds of the Nkporo Shale with *Libycoceras crossense* are probably equivalent to the upper part of the *polyplacum* Zone. *L. crossense* occurs below a horizon elsewhere in southern Nigeria (see Zaborski 1982) containing *L. dandense* (Howarth), of latest Campanian to earliest Maastrichtian age (Howarth 1965: 402–405).

The topmost part of the Nkporo Shale exposed in the Calabar section is probably Lower

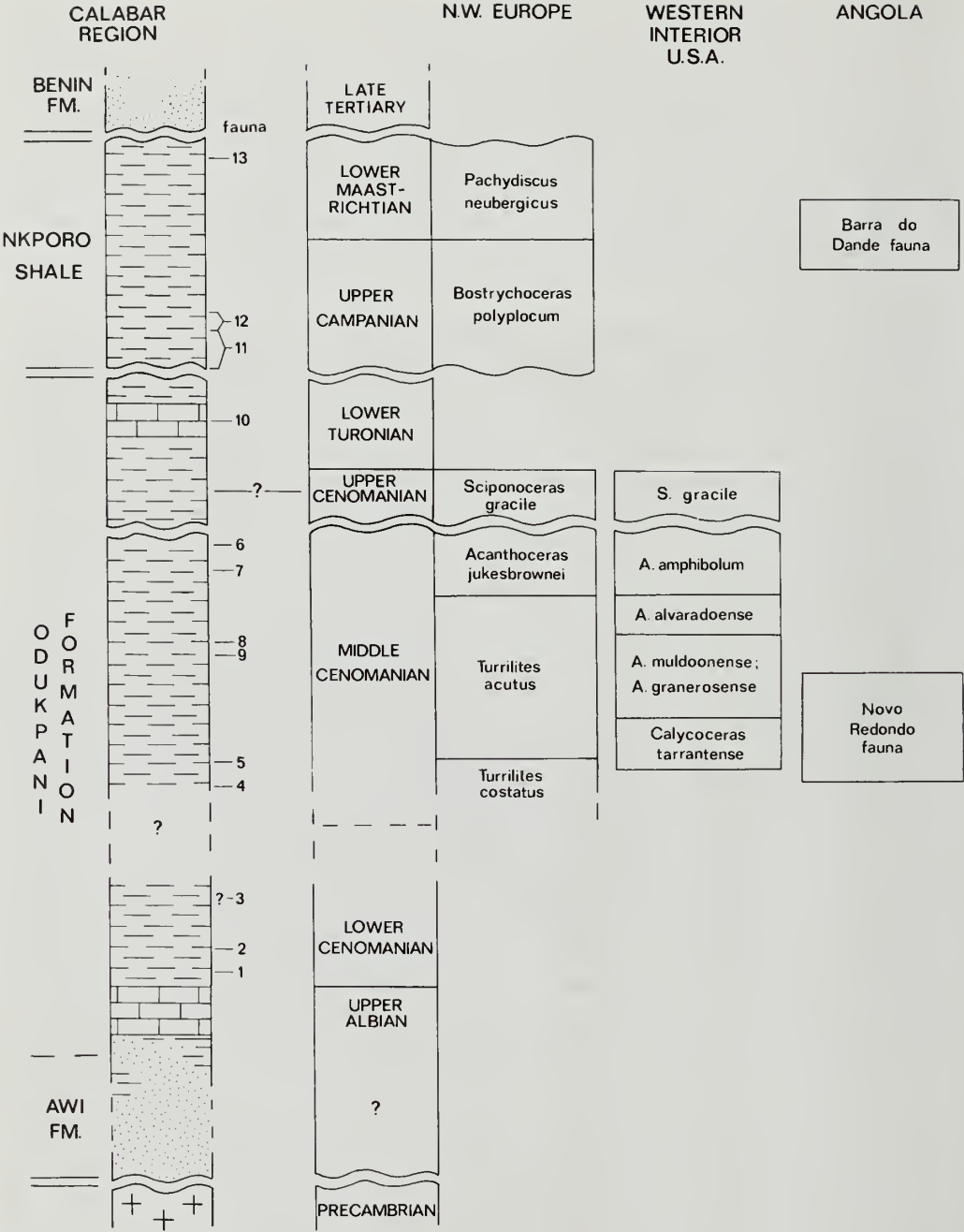


Fig. 66 Generalized sedimentary sequence (not to scale) exposed in the road section north of Calabar and its correlation with north-west Europe, the western interior of the United States and Angola. Zonation in north-west Europe follows Kennedy (1971), Kennedy & Hancock (1978) and Juignet & Kennedy (1976). That for the western interior of the U.S.A. follows Kauffman *et al.* (1978). For Angola, the Barra do Dande fauna is that described by Howarth (1965); the Novo Redondo fauna is that described by Cooper (1973, 1978a).

Maastrichtian. *Sphenodiscus*, a dominantly Maastrichtian genus, is abundant here while *Pachydiscus dossantosi* has its closest affinities with European Lower Maastrichtian pachydiscids, particularly *P. gollevillensis*. This age is in accordance with the evidence provided by the associated inoceramid bivalves *Cordiceramus coxi* (Reyment), *Trochoceras radiosus* (Quaas) and *Endocostea pteroides* (Giers) which range from Upper Campanian to Lower Maastrichtian (A. Dhondt and N. J. Morris, personal communication).

Species of *Libycoceras* provide the most promising basis for correlation in the Nigerian late Campanian and early Maastrichtian. Three zones can be recognized based on the ranges of the successive species *L. afikpoense*, *L. crossense* and *L. dandense* (see Zaborski 1983). These species span the *polyplacum* Zone, with *L. dandense* probably extending into the basal part of the *Pachydiscus neubergicus* Zone. The Zone of *L. afikpoense* is present in the Gombe region of north-east Nigeria, from where Reyment (1955: 90; pl. 19, fig. 3; pl. 20, fig. 4) described juvenile specimens which probably belong to this species. The Zone of *L. crossense* is represented in the Dukamaje Formation of north-west Nigeria which contains forms which are almost certainly conspecific (Zaborski 1982: 312). These occurrences add weight to arguments in favour of a late Campanian marine link between the Gulf of Guinea and the Tethys (see review of this subject in Reyment, 1980), the faunal evidence for which has been weak hitherto.

'*Sphenodiscus studeri* Reyment (1957) may well be closely related to *Libycoceras dandense* (see Zaborski 1982: 325) and a basal Maastrichtian age seems most probable for this species. Reyment's youngest Maastrichtian index species, *Cordiceramus coxi*, occurs in the topmost marine band of the Nkporo Shale in the Calabar section, for which a Lower Maastrichtian age has been suggested above. Neither of Reyment's upper two zones, therefore, seems to be Upper Maastrichtian. The outcropping parts of this substage are dominantly regressive in Nigeria.

Figure 66 shows the generalized sedimentary sequence in the Calabar region and its correlation with north-west Europe, the western interior of the United States and Angola.

Acknowledgements

Thanks are due to Dr M. K. Howarth and Mr D. Phillips for assistance in many ways. Drs A. Dhondt and N. J. Morris kindly identified a number of bivalves. Drs C. W. Wright and W. J. Kennedy provided useful advice. Photographs were supplied by the British Museum (Natural History) Photographic Unit. The Cross River State Government kindly gave permission for necessary field work. This work was completed while the author was in receipt of a University of Ilorin Senate Research Grant.

References

- Adeleye, D. R. & Fayose, E. A. 1978. Stratigraphy of the type section of Awi Formation, Odukpani area, southeastern Nigeria. *J. Min. Geol.*, Ibadan, **15**: 33–37.
- Adkins, W. S. 1928. Handbook of Texas Cretaceous fossils. *Bull. Univ. Tex. Bur. econ. Geol. Technol.*, Austin, **2838**: 1–303, pls 1–37.
- 1929. Some Upper Cretaceous Taylor ammonites from Texas. *Bull. Univ. Tex. Bur. econ. Geol. Technol.*, Austin, **2901**: 203–211, pls 5, 6.
- Anderson, F. M. 1902. Cretaceous deposits of the Pacific Coast. *Proc. Calif. Acad. Sci.*, San Francisco, (3) **2**: 1–154, pls 1–12.
- 1938. Lower Cretaceous deposits in California and Oregon. *Spec. Pap. geol. Soc. Am.*, New York, **16**: 1–339, pls 1–84.
- 1958. Upper Cretaceous of the Pacific Coast. *Mem. geol. Soc. Am.*, New York, **71**: 1–378, pls 1–75.
- Arkell, W. J. *et al.* 1957. Mollusca 4. Cephalopoda, Ammonoidea. In Moore, R. C. (ed.), *Treatise on Invertebrate Paleontology*, L. 490 pp., text-figs. Lawrence, Kansas.
- Barber, W. 1957. Lower Turonian ammonites from north-eastern Nigeria. *Bull. geol. Surv. Nigeria*, Kaduna, **26**: 1–86, pls 1–35.

- Basse, E. 1940. Les céphalopodes crétacés des massifs côtiers syriens. Pt. 1. *Notes Mém. Ht.-Comm. Syrie Liban*, Paris, 3: 412–490, pls 1–9.
- Bayle, E. 1878. Fossiles principaux des Terrains. *Explication Carte géol. Fr.*, Paris, 4 (1): atlas of 158 pls.
- Benavides-Cáceres, V. E. 1956. Cretaceous system in northern Peru. *Bull. Am. Mus. nat. Hist.*, New York, 108: 353–494, pls 31–66.
- Bosc, L. A. G. 1802. Histoire naturelle des coquilles. In Buffon, G. L. L. de, *Histoire naturelle de Buffon*, 5: 1–255, pls 35–44. Paris.
- Böse, E. 1927. Cretaceous ammonites from Texas and northern Mexico. *Bull. Univ. Tex. Bur. econ. Geol. Technol.*, Austin, 2748: 143–312, pls 1–18.
- Boule, M., Lemoine, P. & Thévenin, A. 1906–07. Paléontologie de Madagascar. III – Céphalopodes crétacés des environs de Diégo-Suarez. *Annls Paléont.*, Paris, 1: 173–192, pls 14–20 (1906); 2: 1–56, pls 1–8 (1907).
- Brongniart, A. 1822. Sur quelques terrains de Craie hors du bassin de Paris. In Cuvier, G. & Brongniart, A., *Description géologique des environs de Paris* (nouv. éd.): 80–106. Paris.
- Clark, D. L. 1965. Heteromorph ammonites from the Albian and Cenomanian of Texas and adjacent areas. *Mem. geol. Soc. Am.*, New York, 95: 1–99, pls 1–24.
- Cobban, W. A. 1977. Characteristic marine molluscan fossils from the Dakota Sandstone and intertongued Mancos Shale, west central New Mexico. *Prof. Pap. U.S. geol. Surv.*, Washington, 1009: 1–30, pls 1–21.
- & Hook, S. C. 1980. The Upper Cretaceous ammonite family Coilopoceratidae Hyatt in the Western Interior of the United States. *Prof. Pap. U.S. geol. Surv.*, Washington, 1192: 1–28, pls 1–21.
- & Scott, G. R. 1972. Stratigraphy and ammonite fauna of the Graneros Shale and Greenhorn Limestone near Pueblo, Colorado. *Prof. Pap. U.S. geol. Surv.*, Washington, 645: 1–108, pls 1–41.
- Collignon, M. 1928–29. Les céphalopodes du Cénomanien pyriteux de Diégo-Suarez, Paléontologie de Madagascar. *Annls Paléont.*, Paris, 17: 139–160, pls 15–19 (1928); 18: 1–56, pls 1, 2 (1929).
- 1931. La faune du Cénomanien à fossiles pyriteux du nord de Madagascar. *Annls Paléont.*, Paris, 20: 43–104, pls 5–9.
- 1933. Fossiles Cénomanien d'Antsamatramahavelona (Province d'Analalava, Madagascar). *Annls géol. Serv. Mines Madagascar*, Tananarive, 3: 53–79, 6 figs, pls V–VI.
- 1956. Ammonites néocrétacées du Menabe (Madagascar). IV. Les Phylloceratidae; V. Les Gaudryceratidae; VI. Les Tetragonitidae. *Annls géol. Serv. Mines Madagascar*, Tananarive, 23: 1–106, pls 1–11.
- 1963. *Atlas des fossiles caractéristiques de Madagascar (Ammonites)*. X (Albien). xv+184 pp., pls 241–317. Service géologique, Tananarive.
- 1964. *Atlas des fossiles caractéristiques de Madagascar (Ammonites)*. XI (Cénomanien). xi+152 pp., pls 318–375. Service géologique, Tananarive.
- 1965. Nouvelles ammonites néocrétacées sahariennes. *Annls Paléont.*, Paris, 51: 162–202, 8 pls.
- 1965a. *Atlas des fossiles caractéristiques de Madagascar (Ammonites)*. XIII (Coniacien). vii+88 pp., pls 414–454. Service géologique, Tananarive.
- 1966. Les céphalopodes crétacés du bassin côtier de Tarfaya. *Notes Mém. Serv. géol. Maroc*, Rabat, 175 (2): 7–148, pls 1–35.
- 1969. *Atlas des fossiles caractéristiques de Madagascar (Ammonites)*. XV (Campanien Inférieur). xi+216 pp., pls 514–606. Service géologique, Tananarive.
- Cooper, M. R. 1973. Cenomanian ammonites from Novo Redondo, Angola. *Ann. S. Afr. Mus.*, Cape Town, 62: 41–67, figs 1–13.
- 1978. Uppermost Cenomanian–basal Turonian ammonites from Salinas, Angola. *Ann. S. Afr. Mus.*, Cape Town, 75: 51–152.
- 1978a. The mid-Cretaceous (Albian–Turonian) biostratigraphy of Angola. *Annls Mus. Hist. nat. Nice* 4 (XVI): 1–22, pls 1–6.
- Crick, G. C. 1907. The Cephalopoda from the deposit at the north end of False Bay, Zululand. In Anderson, W., *Third and final report of the Geological Survey of Natal and Zululand*: 163–234, pls 10–15. London.
- Diener, G. 1925. Ammonoidea neocretacea. *Fossilium Cat.*, Berlin, (1: Animalia) 29. 244 pp.
- Douvillé, H. 1904. Paléontologie, mollusques fossiles. In Morgan, J. de, *Mission scientifique en Perse* 3 (4): 191–380, pls 25–50. Paris.
- 1931. Contributions à la géologie de l'Angola. Les ammonites de Salinas. *Bolm Mus. Lab. miner. geol. Univ. Lisb.* 1: 17–46, pls 1–4.

- Erni, A.** 1944. Ein Cenoman-ammonit *Cunningtoniceras höltkeri* nov. spec. aus Neuguinea, nebst Bemerkungen über einige andere Fossilien von dieser Insel. *Eclog. geol. Helv.*, Basel, **37**: 468–475.
- Fabre, S.** 1940. Le Crétacé supérieur de la Basse-Provence occidentale. 1. Cénomanien et Turonien. *Annls Fac. Sci. Marseille* (2) **14**: 1–355, pls 1–10.
- Fayose, E. A.** 1977. Turonian fauna from east of Odukpani, S.E. Nigeria. *Bull. Inst. fond. Afr. noire*, Dakar, (A) **39**: 231–240.
- Forbes, E.** 1846. Report on the Cretaceous fossil invertebrates from southern India, collected by Mr Kaye and Mr Cunliffe. *Trans. geol. Soc. Lond.* (2) **7**: 97–174, pls 7–19.
- Förster, R.** 1978. Evidence for an open seaway between southern and northern proto-Atlantic in Albian times. *Nature, Lond.*, **272**: 158–159.
- & **Scholz, G.** 1979. *Salaziceras nigerianum* n. sp. from southeast Nigeria: faunal evidence for an open seaway between northern and southern Atlantic in late Albian times. *Neues Jb. Geol. Paläont. Mh.*, Stuttgart, **2**: 109–119.
- Gabb, W. M.** 1864–69. *Geological survey of California. Palaeontology*. **1** (4): 57–217, pls 9–32 (1864). **2**: 1–299, pls 1–36 (1869). Philadelphia.
- Gill, J. R. & Cobban, W. A.** 1973. Stratigraphy and geologic history of the Montana Group and equivalent rocks, Montana, Wyoming and North and South Dakota. *Prof. Pap. U.S. geol. Surv.*, Washington, **776**: 1–37.
- Gill, T.** 1871. Arrangement of the families of mollusks. *Smithson. misc. Collns*, Washington, **227**. xvi+49 pp.
- Grossouvre, A. de** 1894. Recherches sur la Craie Supérieure. 2, Paléontologie. Les ammonites de la Craie supérieure. 264 pp., atlas of 39 pls. *Mém. Serv. Carte dét. géol. Fr.*, Paris.
- Guéranger, E.** 1867. *Album paléontologique du département de la Sarthe*. 20 pp., 25 pls. Le Mans.
- Haas, O.** 1942. Some Upper Cretaceous ammonites from Angola. *Am. Mus. Novit.*, New York, **1182**: 1–24.
- 1963. *Paracanthoceras wyomingense* (Reagan) from the Western Interior of the United States and from Alberta (Ammonoidea). *Am. Mus. Novit.*, New York, **2151**: 1–19.
- 1964. *Plesiocanthoceras*, new name for *Paracanthoceras* Haas, 1963, non Furon, 1935. *J. Paleont.*, Tulsa, **38**: 610.
- Hancock, J. M. & Kennedy, W. J.** 1981. Upper Cretaceous ammonite stratigraphy: some current problems. In House, M. R. & Senior, J. R. (eds), *The Ammonoidea*: 531–553. London (Academic Press, for the Systematics Association).
- Hattin, D. E.** 1965. Stratigraphy of the Graneros Shale (Upper Cretaceous) in Central Kansas. *Bull. Kans. Univ. geol. Surv.*, Lawrence, **178**: 1–83, pls 1–5.
- 1968. *Plesiocanthoceras wyomingense* (Reagan) from Graneros Shale and Greenhorn Limestone (Upper Cretaceous) of central Kansas. *J. Paleont.*, Tulsa, **42**: 1084–1090.
- Hauer, F. von** 1858. Über die Cephalopoden der Gosauschichten. *Beitr. Paläont. Oest.*, Vienna, **1**: 7–14, pls 1–3.
- 1866. Neue Cephalopoden aus den Gosagebilden der Alpen. *Sber. Akad. Wiss. Wien* (I) **53**: 300–308, pls 1, 2.
- Henderson, R. A.** 1970. Ammonoidea from the Mata Series (Santonian–Maastrichtian) of New Zealand. *Spec. Pap. Palaeont.*, London, **6**: 1–82, pls 1–15.
- Hoepen, E. C. N. van** 1921. Cretaceous Cephalopoda from Pondoland. *Ann. Transv. Mus.*, Pretoria, **8**: 1–48, pls 1–11.
- Howarth, M. K.** 1965. Cretaceous ammonites and nautiloids from Angola. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **10** (10): 335–412, pls 1–13.
- 1966. A mid-Turonian ammonite fauna from the Moçâmedes Desert, Angola. *Garcia de Orta*, Lisbon, **14**: 217–228, pls 1–3.
- Hyatt, A.** 1894. Phylogeny of an acquired characteristic. *Proc. Am. phil. Soc.*, Philadelphia, **32**: 349–647, pls 1–14.
- 1900. Cephalopoda. In von Zittel K. A. (transl. Eastman, C. R.), *Textbook of Palaeontology*, **1**: 502–604. London.
- 1903. Pseudoceratites of the Cretaceous. *Monogr. U.S. geol. Surv.*, Washington, **44**: 1–351, pls 1–47.
- Imkeller, H.** 1901. Die Kreidebildungen und ihre Fauna am Stallauer Eck und Enzenauer Kopf bei Tölz. *Palaeontographica*, Stuttgart, **48**: 1–64, pls 1–3.
- Jeletzky, J. A.** 1951. Die Stratigraphie und Belemnitenfauna des Obercampen und Maastricht Westfalens, Nordwestdeutschlands und Dänemarks sowie einige allgemeine Gliederungs-Probleme der jüngeren borealen Oberkreide Eurasiens. *Beih. geol. Jb.*, Hannover, **1**: 1–142, pls 1–7.

- Jimbo, K.** 1894. Beiträge zur Kenntnis der Fauna der Kreideformation von Hokkaidō. *Paläont. Abh.*, Jena, **6** (3): 149–194, pls 1–9.
- Jones, D. L.** 1963. Upper Cretaceous (Campanian and Maestrichtian) ammonites from southern Alaska. *Prof. Pap. U.S. geol. Surv.*, Washington, **432**: 1–53, pls 1–41.
- Juignet, P. & Kennedy, W. J.** 1976. Faunes d'ammonites et biostratigraphie comparée du Cénomanien de nord-ouest de la France (Normandie) et du sud de l'Angleterre. *Bull. trimest. Soc. géol. Normandie Amis Mus. Havre* **63** (2): 1–193, pls 1–34.
- Kauffman, E. G., Cobban, W. A. & Eicher, D. L.** 1978. Albion through Lower Coniacian strata, biostratigraphy and principal events, Western Interior, United States. *Annls Mus. Hist. nat. Nice* **4** (XXIII): 1–52, pls 1–17.
- Kellum, L. B. & Mintz, L. W.** 1962. Cenomanian ammonites from the Sierra de Tlahualilo, Coahuila, Mexico. *Contr. Mus. Paleont. Univ. Mich.*, Ann Arbor, **13**: 267–287, pls 1–8.
- Kennedy, W. J.** 1971. Cenomanian ammonites from southern England. *Spec. Pap. Palaeont.*, London, **8**: 1–133, pls 1–64.
- 1978. The middle Cretaceous of Zululand and Natal, eastern South Africa. *Annls Mus. Hist. nat. Nice* **4** (XVIII): 1–29, pls 1–6.
- & **Cobban, W. A.** 1977. Aspects of ammonite biology, biogeography and biostratigraphy. *Spec. Pap. Palaeont.*, London, **17**: 1–94, pls 1–11.
- & **Cooper, M. R.** 1975. Cretaceous ammonite distribution and the opening of the South Atlantic. *J. geol. Soc. Lond.* **131**: 283–288.
- & **Hancock, J. M.** 1970. Ammonites of the genus *Acanthoceras* from the Cenomanian of Rouen, France. *Palaeontology*, London, **13**: 462–490, pls 88–97.
- — 1977. Towards a correlation of the Cenomanian sequences of Japan with those of north-west Europe. *Spec. Pap. palaeont. Soc. Japan*, Tokyo, **21**: 127–141.
- — 1978. The mid-Cretaceous of the United Kingdom. *Annls Mus. Hist. nat. Nice* **4** (V): 1–72, pls 1–30.
- & **Juignet, P.** 1975. Présence du genre *Anagaudryceras* (Ammonoidea) dans le Cénomanien de Haute-Normandie. *C.r. somm. Séanc. Soc. géol. Fr.*, Paris, **1975** (3): 77–79.
- , — & **Hancock, J. M.** 1981. Upper Cenomanian ammonites from Anjou and the Vendée, western France. *Palaeontology*, London, **24**: 25–84, pls 3–17.
- & **Klinger, H. C.** 1975. Cretaceous faunas from Zululand and Natal, South Africa. Introduction, stratigraphy. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **25** (4): 265–315, 1 pl., 12 text-figs.
- — 1979. Cretaceous faunas from Zululand and Natal, South Africa. The ammonite family Gaudryceratidae. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **31** (2): 121–174, pls 1–14.
- & **Wright, C. W.** 1979. On *Kamerunoceras* Reyment, 1954 (Cretaceous Ammonoidea). *J. Paleont.*, Tulsa, **53**: 1165–1178, 4 pls.
- — 1981. *Euhystrioceras* and *Algericeras*, the last mortoniceratine ammonites. *Palaeontology*, London, **24**: 417–435, pls 59–61.
- Klinger, H. C.** 1976. Cretaceous heteromorph ammonites from Zululand. *Mem. geol. Surv. Un. S. Afr.*, Pretoria, **69**. ix+142 pp., 43 pls.
- Kossmat, F.** 1895–98. Untersuchungen über die Südindische Kreideformation. *Beitr. Paläont. Geol. Öst.-Ung.*, Vienna and Leipzig, **9**: 97–203, pls 15–25 (1895); **11**: 1–46, pls 1–8 (1897); **12**: 89–152, pls 14–19 (1898).
- Lamarck, J. B. P. A. de M. de** 1801. *Système des animaux sans vertèbres*. viii+432 pp. Paris.
- Lewy, Z.** 1969. Late Campanian heteromorph ammonites from southern Israel. *Israel J. Earth Sci.*, Jerusalem, **18**: 109–135, pls 1–4.
- 1977. Late Campanian pseudoceratites from Israel and Jordan. *J. palaeont. Soc. India*, Lucknow, **20**: 244–250, 1 pl.
- Mantell, G. A.** 1822. *The fossils of the South Downs*. xvii+327 pp. 42 pls. London.
- Matsumoto, T.** 1954. Family Puzosiidae from Hokkaido and Saghalien. *Mem. Fac. Sci. Kyushu Univ.*, Fukuoka, (D) **5**: 69–118, pls 9–32.
- 1959. Upper Cretaceous ammonites from California. Part 2. *Mem. Fac. Sci. Kyushu Univ.*, Fukuoka, (D) *Spec. vol.* **1**: 1–172, pls 1–41.
- 1967. Evolution of the Nostoceratidae (Cretaceous heteromorph ammonoids). *Mem. Fac. Sci. Kyushu Univ.*, Fukuoka, (D) **18**: 331–347, pls 18–19.
- , **Kawashita, Y., Fujishima, Y. & Miyauchi, T.** 1978. *Mammites* and allied ammonites from the Cretaceous of Hokkaido and Saghalien. *Mem. Fac. Sci. Kyushu Univ.*, Fukuoka, (D) **24**: 1–24, pls 1–6.
- , **Muramoto, T. & Takahashi, T.** 1969. Selected acanthoceratids from Hokkaido. *Mem. Fac. Sci. Kyushu Univ.*, Fukuoka, (D) **19**: 251–296, pls 25–38.

- & **Obata, I.** 1966. An acanthoceratid ammonite from Sakhalin. *Bull. natn. Sci. Mus. Tokyo* **9**: 43–52, 4 pls.
- , **Okada, H., Hirano, B. & Tanabe, K.** 1978. Mid-Cretaceous zonation in Japan. *Annls Mus. Hist. nat. Nice* **4** (XXXIII): 1–23.
- & **Saito, R.** 1954. A nearly smooth pachydiscid from Hokkaido, Japan. *Jap. J. Geol. Geogr.*, Tokyo, **24**: 87–92, pls 9–11.
- , — & **Fukada, A.** 1957. Some acanthoceratids from Hokkaido. *Mem. Fac. Sci. Kyushu Univ.*, Fukuoka, (D) **6**: 1–45, pls 1–18.
- Maury, C. J.** 1930. O Cretaceo da parahyba do norte. *Monografias Div. geol. miner. Bras.*, Rio de Janeiro, **8**: 1–305, pls 1–35.
- Meek, F. B.** 1871. Preliminary paleontological report, consisting of lists of fossils, with descriptions of some new types. *Rep. U.S. geol. geogr. Surv. Territ.*, Washington, **4** (= *Prelim. Rep. U.S. geol. Surv. Wyoming*): 287–318.
- 1876. A report on the invertebrate Cretaceous and Tertiary fossils of the Upper Missouri country. *Rep. U.S. geol. Surv. Territ.*, Washington, **9**. 629 pp., 45 pls.
- & **Hayden, F. V.** 1856. Descriptions of new species of Gasteropoda and Cephalopoda from the Cretaceous formation of Nebraska Territory. *Proc. Acad. nat. Sci. Philad.* **8**: 70–72.
- Moreman, W. L.** 1942. Paleontology of the Eagle Ford Group of north and central Texas. *J. Paleont.*, Tulsa, **16**: 192–220, pls 31–34.
- Morrow, A. L.** 1935. Cephalopods from the Upper Cretaceous of Kansas. *J. Paleont.*, Menasha, **9**: 463–473, pls 49–53.
- Murat, R. C.** 1972. Stratigraphy and palaeogeography of the Cretaceous and Lower Tertiary in southern Nigeria. In Dessauvage, T. F. J. & Whiteman, A. J. (eds), *African Geology*: 251–266. Ibadan.
- Neumayr, M.** 1875. Die Ammoniten der Kreide und die Systematik der Ammonitiden. *Z. dt. geol. Ges.*, Berlin, **27**: 854–892.
- Nwachukwu, S. O.** 1972. The tectonic evolution of the southern portion of the Benue Trough, Nigeria. *Geol. Mag.*, Cambridge, **109**: 411–419.
- Offodile, M. E.** 1976. The geology of the Middle Benue, Nigeria. *Spec. Vol. palaeont. Inst. Univ. Uppsala* **4**: 1–166, pls 1–20.
- & **Reyment, R. A.** 1976. Stratigraphy of the Keana-Awe area of the Middle Benue region of Nigeria. *Bull. geol. Instn Univ. Uppsala* (n.s.) **7**: 37–66, figs 1–41.
- Olade, M. A.** 1975. Evolution of Nigeria's Benue Trough (aulacogen): a tectonic model. *Geol. Mag.*, Cambridge, **112**: 575–583.
- Olsson, A. A.** 1944. Contributions to the paleontology of northern Peru. The Cretaceous of the Paita region. *Bull. Amer. Paleont.*, Ithaca, **28**: 1–164, pls 1–17.
- Orbigny, A. d'** 1840–42. *Paléontologie française, Terrains crétacées*. **1**, *Céphalopodes*: 1–120 (1840), 121–430 (1841), 431–662 (1842), 148 pls. Paris.
- Owen, D. D.** 1852. Descriptions of some new and imperfectly known genera and species of organic remains, collected during the geological surveys of Wisconsin, Iowa and Minnesota. In Owen, D. D., *Report of a geological survey of Wisconsin, Iowa and Minnesota; and incidentally of a portion of Nebraska Territory*: 573–587. Philadelphia.
- Passy, A.** 1832. *Description géologique du département de la Seine-inférieure*. 371 pp., 20 pls. Rouen.
- Pervinquière, L.** 1907. *Carte géologique de la Tunisie. Études de paléontologie tunisienne*, **1**, *Céphalopodes des terrains secondaires*. 438 pp., 27 pls. Paris.
- Petters, S.W.** 1980. Biostratigraphy of Upper Cretaceous foraminifera of the Benue Trough, Nigeria. *J. foramin. Res.*, Washington, **10**: 191–204, 2 pls.
- 1982. Central West African Cretaceous–Tertiary benthic foraminifera and stratigraphy. *Palaeontographica*, Stuttgart, (A) **179**: 1–104, pls 1–15.
- Picard, L.** 1929. On Upper Cretaceous (chiefly Maestrichtian) Ammonoidea from Palestine. *Ann. Mag. nat. Hist.*, London, (10) **3**: 433–456, pls 9, 10.
- Pictet, F. J.** 1863. Discussion sur les variations et les limites de quelques espèces d'ammonites des groupes de *A. rhotomagensis* et *mantelli*. *Mélanges Paléontologiques. Mém. Soc. Phys. Hist. nat. Genève* **17**: 22–58, pls 1–8.
- Ramanathan, R. M. & Kumaran, K. P. N.** 1981. Age and palaeoecology of M-1 well in Calabar Flank, south-eastern Nigeria. *J. Min. Geol.*, Ibadan, **18**: 163–171.
- Reiss, Z.** 1962. Stratigraphy of phosphate deposits in Israel. *Bull. geol. Surv. Israel*, Jerusalem, **34**: 1–23.
- Renz, O.** 1972. Die Gattungen *Puzosia* Bayle, *Bhimaites* Matsumoto und *Desmoceras* Zittel (Ammonoidea) im Oberen Albien Venezuelas. *Eclog. geol. Helv.*, Basel, **65**: 701–724, pls 1–10.

- Reyment, R. A.** 1954. New Turonian (Cretaceous) ammonite genera from Nigeria. *Colon. Geol. Miner. Resour.*, London, **4**: 149–164, pls 1–4.
- 1954a. Some new Cretaceous ammonites from Nigeria. *Colon. Geol. Miner. Resour.*, London, **4**: 248–270, pls 1–5.
- 1955. The Cretaceous Ammonoidea of southern Nigeria and the southern Cameroons. *Bull. geol. Surv. Nigeria*, Kaduna, **25**: 1–112, pls 1–24.
- 1956. On the stratigraphy and palaeontology of the Cretaceous of Nigeria and the Cameroons, British West Africa. *Geol. För. Stockh. Förh.* **78**: 17–96.
- 1957. Über einige wirbellose Fossilien aus Nigerien und Kamerun, Westafrika. *Palaeontographica*, Stuttgart, (A) **109**: 41–70, pls 7–11.
- 1965. *Aspects of the geology of Nigeria*. 145 pp., 18 pls. Ibadan.
- 1980. Biogeography of the Saharan Cretaceous and Paleocene epicontinental transgressions. *Cret. Res.*, London, **1**: 299–327.
- & **Tait, E. A.** 1972. Biostratigraphical dating of the early history of the South Atlantic Ocean. *Phil. Trans. R. Soc.*, London, (B) **264**: 55–95, pls 3–5.
- Sastry, M. V. A., Rao, B. R. J. & Mamgain, V. D.** 1968. Biostratigraphic zonation of the Upper Cretaceous formation of Trichinopoly district, S. India. *Mem. geol. Soc. India*, Bangalore, **2**: 10–17.
- Schlüter, C.** 1871–76. Die Cephalopoden der oberen deutschen Kreide. *Palaeontographica*, Stuttgart, **21**: 1–24, pls 1–18 (1871); **21**: 25–120, pls 19–35 (1872); **24**: 121–264, pls 36–55 (1876).
- Seunes, J.** 1890. Contributions à l'étude des céphalopodes du Crétacé supérieure de la France. 1, Ammonites du calcaire à *Baculites* du Cotentin. *Mém. Soc. géol. Fr. Paléont.*, Paris, **1**: 1–7, pls 1, 2.
- Sharpe, D.** 1853–57. Description of the fossil remains of Mollusca found in the Chalk of England. **1**, Cephalopoda: 1–26, pls 1–10 (1853), 27–36, pls 11–16 (1855), 37–68, pls 17–21 (1857). *Palaeontogr. Soc. (Monogr.)*, London.
- Shimizu, S.** 1934. Ammonites. In Shimizu, S. & Obata, T., *Cephalopoda. Iwanami's lecture series of geology and palaeontology*. 137 pp. Tokyo. [In Japanese].
- 1935. The Upper Cretaceous cephalopods of Japan. Part 1. *J. Shanghai Sci. Inst.* (II) **2**: 159–226.
- Solger, F.** 1904. Die Fossilien der Mungokreide in Kamerun und ihre geologische Bedeutung, mit besonderer Berücksichtigung der Ammonitiden. In Esch, E., Solger, F., Oppenheim, M. & Jäkel, O., *Beiträge zur Geologie von Kamerun*: 83–242, pls 3–5. Stuttgart.
- Sowerby, J. de C.** 1823–46. *The mineral conchology of Great Britain* (cont.) **4** (pars)-7, pls 384–648. London.
- Spath, L. F.** 1922. On the Senonian ammonite fauna from Pondoland. *Trans. R. Soc. S. Afr.*, Cape Town, **10**: 113–147, pls 5–9.
- 1923–43. A monograph of the Ammonoidea of the Gault. 787 pp., 72 pls. *Palaeontogr. Soc. (Monogr.)*, London.
- 1923a. Appendix II. On the Ammonite Horizons of the Gault and Contiguous Deposits. *Summ. Progr. geol. Surv. Lond.* **1922**: 139–149.
- 1925. On Upper Albian Ammonoidea from Portuguese East Africa. With an appendix on Upper Cretaceous ammonites from Maputoland. *Ann. Transv. Mus.*, Pretoria, **11**: 179–200, pls 28–37.
- 1926. On new ammonites from the English Chalk. *Geol. Mag.*, London, **63**: 77–83.
- Stephenson, L. W.** 1941. The larger invertebrate fossils of the Navarro Group of Texas. *Publs Bur. econ. Geol. Univ. Tex.*, Austin, **4101**: 1–641, pls 1–95.
- 1952. Larger invertebrate fossils of the Woodbine Formation (Cenomanian) of Texas. *Prof. Pap. U.S. geol. Surv.*, Washington, **242**: 1–226, pls 1–59.
- 1955. Basal Eagle Ford fauna (Cenomanian) in Johnson and Tarrant Counties. *Prof. Pap. U.S. geol. Surv.*, Washington, **274-c**: 53–67, pls 4–7.
- Stoliczka, F.** 1863–66. The fossil Cephalopoda of the Cretaceous rocks of southern India. *Mem. geol. Surv. India Palaeont. indica*, Calcutta, (3) **1**: 41–56, pls 26–31 (1863); **2-5**: 57–106, pls 32–54 (1864); **6-9**: 107–154, pls 55–80 (1865); **10-13**: 155–216, pls 81–94 (1866).
- Thomel, G.** 1969. Réflexions sur les genres *Eucalycoceras* et *Protacanthoceras* (Ammonoidea). *C.r. hebd. Séanc. Acad. Sci.*, Paris, (D) **268**: 649–652.
- 1972. Les Acanthoceratidae Cénomaniens des chaînes subalpines méridionales. *Mém. Soc. géol. Fr.*, Paris, (n.s.) **116**: 1–204, pls 1–85.
- Tuomey, M.** 1856. Description of some new fossils from the Cretaceous rocks of the southern states. *Proc. Acad. nat. Sci. Philad.* **7**: 162–172.
- Usher, J. L.** 1952. Ammonite fauna of the Upper Cretaceous of Vancouver Island, British Columbia. *Bull. geol. Surv. Can.*, Ottawa, **21**: 1–182, pls 1–30.
- Venzo, S.** 1936. Cefalopodi del Cretacea medio-superiore dello Zululand. *Palaeontogr. ital.*, Pisa, **36**: 59–133, pls 5–12.

- Ward, P. D. & Mallory, V. S. 1977. Taxonomy and evolution of the lytoceratid genus *Pseudoxybeloceras* and relationship to the genus *Solenoceras*. *J. Paleont.*, Tulsa, **51**: 606–618, 3 pls.
- Wedekind, R. 1916. Über Lobus, Suturallobus und Inzision. *Centbl. Miner. Geol. Paläont.*, Stuttgart, **1916** (8): 185–195.
- Whiteaves, J. F. 1895. Notes on some fossils from the Cretaceous rocks of British Columbia. *Can. Rec. Sci.*, Montreal, **6**: 313–318.
- 1903. On some additional fossils from the Vancouver Cretaceous, with a revised list of species therefrom. *Mesozoic Fossils* **1** (5): 309–415, pls 40–51. Geological Survey of Canada, Ottawa.
- Wiedmann, J. 1962. Ammoniten aus der Vascogotischen Kreide (Nordspanien). 1, Phylloceratina, Lytoceratina. *Palaeontographica*, Stuttgart, (A) **118**: 119–237, pls 8–14.
- & Kauffman, E. G. 1978. Mid-Cretaceous biostratigraphy of northern Spain. *Annls Mus. Hist. nat. Nice* **4** (III): 1–34, pls 1–12.
- & Kullman, J. 1981. Ammonoid sutures in ontogeny and phylogeny. In House, M. R. & Senior, J. R. (eds), *The Ammonoidea*: 215–255. London (Academic Press, for the Systematics Association).
- Wright, C. W. 1952. A classification of the Cretaceous ammonites. *J. Paleont.*, Tulsa, **26**: 213–222.
- 1963. Cretaceous ammonites from Bathurst Island, Northern Australia. *Palaeontology*, London, **6**: 597–614, pls 81–89.
- & Kennedy, W. J. 1981. The Ammonoidea of the Plenus Marls and the Middle Chalk. 148 pp., 32 pls. *Palaeontogr. Soc. (Monogr.)*, London.
- & Matsumoto, T. 1954. Some doubtful Cretaceous ammonite genera from Japan and Saghalien. *Mem. Fac. Sci. Kyushu Univ.*, Fukuoka, (D) **4**: 107–134, pls 7, 8.
- & Wright, E. V. 1951. A survey of the fossil Cephalopoda of the Chalk of Great Britain. 40 pp. *Palaeontogr. Soc. (Monogr.)*, London.
- Yabe, H. 1903. Cretaceous Cephalopoda from Hokkaido. Part 1. *J. Coll. Sci. imp. Univ. Tokyo* **18** (2): 1–55, pls 1–7.
- Young, G. & Bird, J. 1828. *A geological survey of the Yorkshire coast*. 367 pp., 19 pls. Whitby.
- Young, K. 1963. Upper Cretaceous ammonites of the Gulf Coast of the United States. *Bull. Univ. Tex. Bur. econ. Geol. Technol.*, Austin, **6304**: 1–373, pls 1–82.
- & Powell, J. D. 1978. Late Albian–Turonian correlations in Texas and Mexico. *Annls Mus. Hist. nat. Nice* **4** (XXV): 1–36, pls 1–9.
- Zaborski, P. M. P. 1982. Campanian and Maastrichtian sphe nodiscid ammonites from southern Nigeria. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **36** (4): 303–332, 36 figs.
- 1983. Campano-Maastrichtian ammonites, correlation and palaeogeography in Nigeria. *J. afr. Earth Sci.*, Oxford, **1**: 59–63.
- Zittel, K. A. von 1884. Cephalopoda. In: *Handbuch der Palaeontologie*, **1** (Abt. 2, Lief. 3): 329–522. Munich and Leipzig.
- 1895. *Grundzüge der Palaeontologie (Palaeozoologie)*. vii+972 pp. Munich and Leipzig.

Note added in proof

Kennedy & Wright (1984) have recently reviewed the genus *Coilopoceras* and conclude that it is primarily a late Turonian form. They could find no good evidence for its occurrence before the middle Turonian. In view of their findings, it is possible that the uppermost exposed part of the Odukpani Formation in the Calabar region is somewhat younger than the early Turonian age suggested in this work.

Kennedy, W. J. & Wright, C. W. 1984. The Cretaceous ammonite *Ammonites requienianus* d'Orbigny, 1841. *Palaeontology*, London, **27**: 281–293, pls 35–37.

Index

New taxonomic names and the page numbers of the principal references are in **bold** type. An asterisk (*) denotes a figure.

- Aba 5*
- Acanthoceras* **33-9**
alvaradoense 38; Zone 62*
amphibolium 4, 34*, **35-8**, 36*, 37*, 39, 42, 51, 59-60; Zone 62*
crassiornatum 33
cunningtoni 42
var. *cornuata* 38, 40
var. *inermis* 40
eschii 51
eulessanum 42-3
evolutum 40; aff. *evolutum* 40
expansum 33
flexuosum 33
granerosense 59; Zone 62*; cf. *granerosense* 60
haughi 30
hazzardi 35
hippocastanum 33
jukesbrownei assemblage 35; Zone 59, 62*
latum 33
lonsdalei 42
meridionale 42
var. *multicostata* 42
muldoonense 51, 59-60; Zone 43, 62*
munitum 33
newboldi 31, 33
quadratum 33
nigeriense 58
robustum 4, **33-5**, 34*, 59
rhotomagense 33; Zone 59
var. *sussexiensis* 40, 59
sussexiensis 40
sp. 4, 37. **38-9**
- Acanthocerataceae* 22-58
Acanthoceratidae 26-53
Acanthoceratinae 33-9
Acompsocheras **29-30**, 58
ansatramahaveloense 29
calabarensis 3, 27*, **29**, 31*
catzigrasae 29
essendiense 29, 58; aff. *essendiense* 3
pseudosarthense 29
renevieri 29-30; aff. *renevieri* 3, **30**, 31*, 58
sahnii 29
sarthense 29
subwaterloti 29, 58
tenue 29
viotti 29
- Afikpo 20
Africa 2
north 42
western 4, 42
Akanu 13
Akamkpa, see Calabar-Akamkpa road
- Albian 3, 5*, 19, 58, 60-1
Upper 3, 62*
- Albian-Cenomanian boundary 58
Algeria 53, 61
Ammonites austeni 17
bochumensis 29
buddha 5
cooperi 16
cunningtoni 42, 45
Egertoni 19
egertonianus 19
euomphalus 39
harpax 30
largilliertianus 22
laticlavus 26
lenticularis 57
lobata 57
meridionalis 42-3
mitis 8
neubergicus 19
obtectus 22
renevieri 30
rhotomagensis 33, 40
sacya 5, 7
subobtectus 22
sussexiensis 49
- Anagaudryceras* **5-8**
buddha 7
involutum 4, 6*, **7-8**, 59
mikobokense 8
poliissimum 8
sacya 7
utaturensis 7
yamashitai 8
- Anaklinoceras* 16; see *Nostoceras*
Anapuzosia 17; see *Puzosia*
Ancylloceras cheyennense 17
lineatus 11, 13
nebrascense 14
- Angola 2, 7, 19, 26, 49, 59-60, 62*, 63; see also Barra do Dande, Luanda, Nova Redondo
- Anisoceras cooperi* 14, 16
Ariyalur Group 61
Atlantic Ocean, North 60
South 4, 60
Austiniceras dibleyi 17, 19
Australasia 42
Awi Formation 3, 5*, 59, 62*
- Baculites* sp. 4
Barra do Dande fauna 62*
Benin Formation 3, 4*, 62*
Benue Valley 3, 61
Bostrychoceras 14, 61
polyplacum Zone 61, 62*, 63
Brazil 22
British Museum (Natural History) 5, 63
- Calabar, 2-3, 5, 5*, 7-8, 10-11, 13-14, 17, 19-20, 22, 24, 26, 32-3, 35, 38, 40, 43, 45, 49, 53, 55, 57, 59, 61, 62*, 63, 69
Calabar-Akamkpa road 3, 5*, 26, 29-30
Calabar-Ikot Ekpene road 3-5, 5*, 26, 29-30
Calycceras 4, **32-3**, 58
newboldi 33, 59; see also *Mantelliceras mantelli*
(*Conlinoceras*) 32-3
tarrantense Zone 59, 62*
(*Newboldiceras*) **32-3**
annulatum 4, **32-3**, 32*, 34*, 59-60
- Cameroun 5*
- Campanian 10, 13, 61
late 63
Lower 11, 13-14
Upper 3, 4*, 10, 13-14, 17, 19, 61, 62*, 63
- Cenomanian 2, 58, 60-1
late 3, 26
Lower 3, 26, 29-30, 33, 58, 61, 62*
Middle 3, 7, 10-11, 19, 22, 24, 26, 32-3, 35, 38, 40, 43, 45, 49, 59-61, 62*
- Upper 30, 33, 60, 62*
- Chalk 19
Christophoceras 13
ramboulei 13
Cirroceras 14
Coahuilites 58
Coilopoceras **53-7**, 61, 69
colleti 53, 61
discoideum 57
inflatum 57, 61
newelli, 4, 55, 57, 61; aff. *newelli* 54*, **55-7**, 55*, 56*, 61
- Coilopoceratidae* 53-7
Colorado 43, 59, 60
Coniacian 10, 13, 61
Conlinoceras 32-3; see *Calycceras*
Cordiceramus coxi 63; Zone 61
Cross River State Government 63
Cuanza Basin 60
Cunningtoniceras cunningtoni 42
höltkeri 42
Cyphoceras 11; see *Pseudoxybeloceras*
- Desmoceras latidorsatum* 58
sp. 3
(*Pseudouhligella*) *calabarensis* 58
sp. 3
Desmocerataceae 17-22
Desmoceratidae 17-19

- Dhondt, Dr A. 63
Didymoceras **14–17**, 61
 cheyennense 17, 61; aff. *cheyennense* 4, 15*, **17**
 fresnoense 17
 hornbyense 16, 61; aff. *hornbyense* 4, 12*, **14–17**, 15*
 kernense 16
 whiteavesi 14, 16
 dimorphism 26, 57
 dissolution 3, 58
 Dukamaje Formation 63
- Endocostea pteriodes* 63
 England 19, 26
 southern 35, 38, 58–60
Euhystriochoceras 58
 occidentale Zone 58
Euomphaloceras **39–51**
 asura 51
 cunningtoni 40, **42–51**, 59–60
 alatum 4, 43, **49–51**, 50*, 52*, 59
 cunningtoni 3, 38, 43, **45–9**, 46*, 47*, 51, 59–60
 lonsdalei 43, 60
 meridionale 3, 41*, 42, **42–5**, 44*, 48–9, 60
 cornutum 38, 52
 euomphalum 42
 var. *pervinquieri* 42
 inermis 3, **40**, 41*, 59–60
 lehmanni 51
 lonsdalei 42–3, 49
 meridionale 42–3
 multicostatum 51
 septemseriatum 3
Euomphaloceratinae 39–52
 Europe 42
 north-west 20, 33, 60, 62*, 63
 western 59, 61
Exiteloceras bennisoni 17
 desertense 16
 Eze-Aku Formation 61
- folding 3, 5*, 59–61
Forbesiceras **22–6**, 58
 conlini 26; aff. *conlini* 58
 largilliertianum 26; aff. *largilliertianum* 26
 obtectum 3–4, **22–6**, 23*, 24*, 25*, 27*, 59–60
 sculptum 58
 subobtectum 3, **22**, 23*, 26
 sp. 3
Forbesiceratidae 22–6
 France 40; see also Rouen, Normandy
 northern 59
 north-west 7, 26, 33, 59
 western 26
- Gaudryceras* **8–10**
 analabense 10
 beantalyense 4, **8–10**, 9*
 cinctum 10
 densiplicatum 8
 mite 8, 10
 propemite 10
 tenuiliratum 8
 varagurense 8
 varicostatum 4, **10**, 61
Gaudryceratidae 5–10
Glebosoceras 57
 glebosum 57
 Gombe 63
 Graneros Shale 59
 Gulf of Guinea 63
- Hamites clinensis* 13
 vancouverensis 16
 hardground 58
Haughiceras 30; see *Pseudocalycoceras*
Heteroceras Cheyennense 17
 hornbyense 14, 16
 perversum 16
 Hokkaido 13
Hoplitoides crassicosatus 53
 ingens 57
 Howarth, Dr M. K. 63
Hypoturrillites carcitensis Zone 58
- Ikot Ekpene 4*; see Calabar-Ikot Ekpene road
 Ilorin, University of 5, 63
 India 42, 61
 southern 7
 inoceramid bivalves 63
- Japan 38, 42, 59–60; see also Hokkaido
Kamerunoceras **51–3**
 tinrhertense 4, **51–3**, 52*, 54*, 61
 turonense 53
 Kennedy, Dr W. J. 63
- Libyoceras* 3, 63
 afikpoense 4, 63; Zone 61, 63
 crossense 4, 61, 63; Zone 63
 dandense 61, 63
 ismaelis 61
 'Lower Limestone' 58
 Luanda 60
- Maastrichtian 13, 61–2
 early 63
 Lower 3, 4*, 8, 13, 20, 57, 61, 62*, 63
 Upper 61, 63
 macroconch 26, 58
 Malagasy Republic 10–11, 13, 42
Mantelliceras mantelli and *Calycoceras newboldi* Zone 33
 saxbii Zone 58
Mantelliceratinae 26–33
 marine link 63
Metengonoceras dumbli 3
- Metoicoeras* 58
 geslinianum 60
 aff. *ornatum* 60
 Mfamosing Quarry 3, 5*, 58–9
 Limestone Formation 58
 microconch 26, 58
 Middle East 42, 61
 migration, faunal 60
 Morocco 38
 Morris, Dr N. J. 63
Mortoniceras 58
- Neodesmoceras* 10
 New Zealand 10, 13
Newboldiceras 32; see *Calycoceras*
 Nkporo Shale 3–4, 4*, 8, 10, 13–14, 17, 19–20, 57, 61, 62*, 63
 Normandy 59
Nostoceras 4, 14, 16
 hornbyense 14
 mexicanum 16
 (*Anaklinoceras*) 16
 Novo Redondo 26, 60; fauna 62*
- Oban Massif 2
 Odukpani Formation 3–4, 5*, 7, 10–11, 19, 22, 24, 26, 29–30, 32, 35, 38, 43, 45, 49, 53, 55, 57–61, 62*, 69
- Pachydiscidae* 19–22
Pachydiscus **19–22**
 dossantosi 4, 13, 18* **20–2**, 21*, 63
 egertoni 4, **19–20**, 21* 61
 egertonianus 19
 endymion 22
 gettyi 22
 gollevillensis 20, 22, 63
 jacquoti 22
 neubergicus 20, 22, 61; Zone 62*, 63
 stallauensis 20; aff. *stallauensis* 19–20
 Pacific Coast, North America 13, 16, 61
Paracanthoceras amphibolum 35
Parapachydiscus dossantosi 20
 sp. 20
Parasolenoceras 11; see *Pseudoxybeloceras*
 Peru 22, 55, 61
 Phillips, D. 63
Phylloceras cf. *velledae* 58
Plesiocanthoceras amphibolum 35
 wyomingense 38
Polyaspidoceras 53
 shimizui 53
 Precambrian 3, 62*
Pseudocalycoceras **30–2**, 61
 angolaense 31
 dentonense 31
 harpax 31
 haughi 30; cf. *haughi* 4, **30–2**, 31*, 60
 morpheus 31

- paralouitense* 31
 (Haughicerias) *haughi* 30
Pseudouhligella, see *Desmoceras*
Pseudoxybeloceras 11–14
bicostatum 13
compressum 13
 (Cyphoceras) 11, 13
nanaimoense 13
 (Parasolenoceras) 11, 13, 61
bicostatum 14
clinensis 14
compressum 14
lineatum 14
nanaimoense 14
ramboulei 14
splendens 11, 13–14; aff. *splendens* 4, 12*, 13–14
Puzosia 17–19
buenaventura 17
matheroni 17
 sp. 3–4, 58
 (Anapuzosia) 17–19
colusaensis 19
dibleyi 19; cf. *dibleyi* 3–4, 17–19, 18*, 60
multicostata 19
saintoursi 19
Puzosiinae 17–19

 Rouen 33, 35; fossil bed 26, 35, 40

 Sahara 4, 53

 Santonian 13, 61
Sciponoceras gracile faunal assemblage 60
 Zone 61, 62*
Sharpeiceras 3, 26–9, 58
congo 28
corroyi 28
falloii 28
florenceae 28
goliath 28, 60
laticlavium 28–9, 58, 60
nigeriense 3, 25*, 26–9, 27*, 58
 var. *indica* 29
 var. *mexicanum* 29
occidentale 28
piveteaui 28
schlueteri 28
tlahualiloense 28
vohipalense 28
Solenoceras 11, 13
 South Africa 10; see also Zululand
 Sphenodiscidae 57–8
Sphenodiscus 3, 13, 57–8, 63
lobatus 61
costatus 4, 56*, 57–8
lobatus 4
pleurisepta 58
studerii 63; Zone 61

 Taylor Formation 13
 Tertiary, see Benin Formation

 Tethys 63
 Tetragonitaceae 5–10
 Texas 13, 26, 38, 43, 60
 Thatcher Limestone Member 59
Trochoceras *radius* 63
 Turrititaceae 10–17
 Turritites 10–11
acutus 4, 11, 59–60; assemblage 35; Zone 35, 59–60, 62*
costatus 3, 10–11, 12*, 58–60; Zone 33, 58–60, 62
scheuchzerianus 3, 7*, 10, 11, 12*, 59; Zone 58
 Turrititidae 10–17
 Turrititinae 10–11
 Turonian 3, 55, 57, 59, 61
 early 3, 69
 mid 61, 69
 late 61, 69
 Lower 5*, 53, 55, 60–1, 62*

 unconformity 3, 60–1
 United States 22, 42, 61; see also Texas, Colorado
 western interior 38, 43, 57, 59, 61, 62*, 63

 Wright, Dr C. W. 63

 Zululand 33, 35